EFFECTIVE CONSERVATION OF MELANISTIC LIZARD SPECIES IN THE GREATER CEDERBERG BIODIVERSITY CORRIDOR

Dahné A. Janse van Rensburg

Dissertation presented for the degree of Doctor of Philosophy

at Stellenbosch University

Supervisor: Prof. P. le Fras N. Mouton

Co-supervisor: Prof. J.H. van Wyk

December 2009

DECLARATION:

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ABSTRACT

The Cape Floristic Region (CFR) is a biodiversity hotspot in South Africa, threatened by climate change and various other processes. The Greater Cederberg Biodiversity Corridor (GCBC) is a conservation area incorporating both public and private land, providing a practical and effective solution to conserve biodiversity in the CFR. This area is also home to two of the eight melanistic cordylid lizard species found in south-western South Africa. One of the herpetological conservation targets identified for the GCBC was an understanding of the ecology of melanistic cordylid populations with particular reference to global environmental change.

Most melanistic cordylids occur in cool coastal and montane localities, and it was suggested that melanism has a thermoregulatory function in these species. The first aim of this study was to determine the climatic conditions with which melanistic cordylids are currently associated. Several melanistic cordylid populations showed a distinct association with a high incidence of fog and cloud cover, underscoring the thermal melanism hypothesis, which predicts that melanistic lizards should occur in cool environments. Several other populations, however, did not show such an association.

The next aim was thus to compare habitat use and morphology among 10 melanistic cordylid populations. Individuals of the northern population of *Pseudocordylus capensis* and the *Cordylus peersi* population occurred in the warmest environments, used significantly higher rock formations, and had relatively longer limbs than those of other melanistic populations. Having a morphology that allows for flexibility in habitat use, may enable species such as *P. capensis* to overcome the constraints of melanism in warm environments.

Being melanistic may result in decreased activity times in warm environments. The variation in habitat thermal quality and daily activity patterns of two melanistic cordylid

species with different morphologies and habitat preferences, occurring sympatrically, was investigated. During summer, high rocks provided a better thermal quality habitat to *P. capensis* than small rocks, and *P. capensis* had a longer activity period than *C. oelofseni*. This suggests that the thermal opportunities provided by high rock enables *P. capensis* to increase its activity time.

The impact of terrestrial and aerial predators can help shape body armour in lizards, with those species more exposed to aerial predators being faster and less armoured, and those more exposed to terrestrial predators being more heavily armoured. The degree of body armour in melanistic cordylids and their non-melanistic relatives was investigated. Melanistic members of the *cordylus-niger-oelofseni* and *C. polyzonus* clades had less armour than their non-melanistic relatives, supporting the prediction that melanistic cordylids basked more and were more exposed to aerial predators than non-melanistic lizards. An increase in body armour in *C. peersi* indicated exposure to terrestrial predators, whereas *P. capensis* had a reduction in body armour, indicating exposure to aerial predators. Little body armour, together with a slender morphology and long limbs, may thus enable this species to move with ease on large boulders and scale vertical surfaces to successfully avoid predators.

Pseudocordylus capensis displayed much greater movement rates during activity than other cordylids. A less sedentary foraging strategy may be a prerequisite for life on large, barren rock surfaces where food availability may be low or not uniformly distributed. Both males and females of this species also had large home ranges, a unique phenomenon for cordylids. Space use of males only overlapped marginally, but extensive overlap among males and females and among females, respectively, was observed.

Due to the constraining effect of climate on the distribution of most melanistic populations, melanistic cordylids should be considered as priority species for conservation.

While *P. capensis* is pre-adapted for survival in warm climates, it is dependent on the availability of suitable habitats. The GCBC would thus play an important role in the conservation of this species' habitat.

UITTREKSEL

Die Kaapse Blommeryk (KBR) is ‘n “biodiversity hotspot” in Suid-Afrika wat deur klimaatsverandering en verskeie ander prosesse bedreig word. Die Groter Cederberg Biodiversiteitskorridor (GCBK) is ’n bewaringsarea wat beide openbare en privaatgrond inkorporeer, en ’n praktiese en effektiewe oplossing tot die bewaring van biodiversiteit in die KBR bied. Twee van die ag melanistiese gordelakkedisse wat in suidwestelike Suid-Afrika aangetref word, kom ook hier voor. Een van die herpetologiese bewaringsdoelwitte vir die GCBK was om insig oor die ekologie van melanistiese gordelakkedis populasies met verwysing na globale omgewingsveranderinge in te win.

Die meeste melanistiese gordelakkedisse kom in koel kus- en berggebiede voor, en daar is voorgestel dat melanisme ‘n termoregulerende funksie by hierdie spesies het. Die eerste doel van die studie was om die huidige klimaatstoestande waarmee melanistiese gordelakkedisse geassosieer word, te bepaal. Verskeie melanistiese gordelakkedis-populasies het ‘n duidelike assosiasie met mis en wolkdekking getoon, wat die termiese melanisme hipotese se voorspelling dat melanistiese akkedisse in koue omgewings moet voorkom, ondersteun. Verskeie ander populasies, het egter nie so ‘n assosiasie getoon nie.

Die volgende doel was om habitatgebruik en morfologie tussen 10 melanistiese gordelakkedispopulasies vergelyk. Individue van die noordelike populasie van *Pseudocordylus capensis* en *Cordylus peersi* het in die warmste omgewings voorgekom, het relatief langer ledemate gehad en beduidend hoër rotsformasies as ander melanistiese populasies benut. ’n Morfologie wat buigsame gebruik van die habitat toelaat, kan sommige spesies soos *P. capensis* in staat stel om die beperkinge van melanisme in ‘n warm omgewing te oorkom.

In warm omgewings mag melanisme tot ’n afname in aktiwiteitstye lei. Variasie in termiese kwaliteit van die habitat en daaglikse aktiwiteitspatrone van twee melanistiese

spesies, met verskillende morfologieë en habitatvoorkeure, wat simpatries voorkom is bestudeer. Gedurende somer het hoë rotse ‘n beter termiese kwaliteit habitat aan *P. capensis* verskaf as die klein rotse, en *P. capensis* het ‘n langer aktiwiteitsperiode as *C. oelofseni* gehad. Dit stel voor dat die termiese geleenthede wat deur hoë rotse verskaf word, *P. capensis* in staat stel om sy aktiwiteitsperiode te verleng.

Die invloed van terrestriële en lugpredatore kan help om liggaamspantser in akkedisse te vorm. Spesies wat hoofsaaklik aan lugpredatore blootgestel is, is vinniger en het minder pantser, terwyl spesies wat hoofsaaklik aan terrestriële predatore blootgestel is, meer pantser het. Die graad van pantser in melanistiese gordelakkedisse en hulle nie-melanistiese naasverwantes is ondersoek. Melanistiese lede van die *cordylus-niger-oelofseni* en *C. polyzonus* klades het minder pantser as hulle nie-melanisties naasverwantes gehad, en ondersteun die voorspelling dat melanistiese gordelakkedisse meer in die son gebak het en meer aan lupredatore blootgestel was. ’n Toename in pantser by *C. peersi* dui op blootstelling aan terrestriële predatore, terwyl *P. capensis* die minste pantser van alle melanistiese gordelakkedisse het, wat dui op blootstelling aan lugpredatore. Min beskerming, tesame met ‘n lenige morfologie en lang ledemate, mag dus hierdie spesie toelaat om gemaklik oor groot rotse en vertikale oppervlaktes te beweeg en roofdiere suksesvol te vermy.

Pseudocordylus capensis het groter bewegingstempo’s tydens aktiwiteit as ander gordelakkedisse getoon. ‘n Meer beweeglike voedingstrategie mag ook ‘n voorvereiste wees vir ‘n lewe op groot, leë klipoppervlaktes waar voedselbeskikbaarheid dalk laag kan wees en nie eweredig versprei is nie. Beide mannetjies en wyfies het ook groot tuisgebiede gehad, ’n unieke verskynsel by gordelakkedisse. Mannetjies se ruimtes het slegs marginaal oorvleuel, terwyl daar heelwat oorvleueling tussen mannetjies en wyfies se ruimtes was.

As gevolg van die beperkende invloed van klimaat op die verspreiding van die meeste melanistiese populasies, moet melanistiese gordelakkedisse as prioriteitspesies vir bewaring beskou word. Terwyl *P. capensis* pre-aangepas is vir oorlewing in warm klimate, is hierdie spesie afhanklik van die beskikbaarheid van gepaste habitatte. Die GCBK sal dus ’n belangrike rol vervul in die bewaring van die habitat van hierdie spesie.

ACKNOWLEDGMENTS

Completing a thesis is not something one can achieve without the help and assistance of many other people. One's supervisor is probably the most important of all these people. During my studies I received lots of funny and interesting e-mails referring to postgraduate studies, but this particular one really caught my attention:

"The Rabbit's Thesis

One sunny day a rabbit came out of her hole in the ground to enjoy the fine weather. The day was so nice that she became careless and a fox snuck up behind her and caught her.
"I am going to eat you for lunch!" said the fox.
"Wait!" replied the rabbit, "You should at least wait a few days."
"Oh yeah? Why should I wait?"
"Well, I am just finishing my thesis on 'The Superiority of Rabbits over Foxes and Wolves'."
"Are you crazy? I should eat you right now! Everybody knows that a fox will always win over a rabbit."
"Not really, not according to my research. If you like, you can come into my hole and read it for yourself. If you are not convinced, you can go ahead and have me for lunch."
"You really are crazy!" But since the fox was curious and had nothing to lose, it went with the rabbit. The fox never came out.

A few days later the rabbit was again taking a break from writing and sure enough, a wolf came out of the bushes and was ready to set upon her.
"Wait!" yelled the rabbit, "You can't eat me right now."
"And why might that be, my furry appetizer?"

"I am almost finished writing my thesis on 'The Superiority of Rabbits over Foxes and Wolves'."

The wolf laughed so hard that it almost lost its grip on the rabbit. "Maybe I shouldn't eat you; you really are sick...in the head. You might have something contagious."

"Come and read it for yourself; you can eat me afterward if you disagree with my conclusions."

So the wolf went down into the rabbit's hole and never came out.

The rabbit finished her thesis and was out celebrating in the local lettuce patch. Another rabbit came along and asked, "What's up? You seem very happy."

"Yup, I just finished my thesis."

"Congratulations. What's it about?"

"'The Superiority of Rabbits over Foxes and Wolves'."

"Are you sure? That doesn't sound right."

"Oh yes. Come and read it for yourself." So together they went down into the rabbit's hole.

As they entered, the friend saw the typical graduate abode, albeit a rather messy one after writing a thesis. The computer with the controversial work was in one corner. And to the right there was a pile of fox bones, on the left a pile of wolf bones. And in the middle was a large, well-fed lion.

The Moral of the Story: The title of your thesis doesn't matter. The subject doesn't matter. The research doesn't matter. All that matters is who your advisor is.**”**

I was really privileged to have met le Fras Mouton during my undergraduate studies and to have had him as my postgraduate supervisor for several years. I would like to express my sincere gratitude towards him for all his encouragement, patience and support, his

understanding, useful advice and helpful discussion, and all the wonderful music he introduced me to. Thank you for introducing me to the world of herpetology! And thank you for being the lion in my story!

I also wish to express my thanks to the following people and institutions:

- My co-supervisor, Hannes van Wyk, for his helpful inputs and comments, and providing me with a better understanding of thermoregulation.
- Adriaan van Niekerk (Geography Department), for his help with the GIS analysis.
- Laco Mucina, for his help with the analyses of the climatic data.
- Alex Flemming, for his help with the histology of cordylid osteoderms.
- Alex Kisters (Geology Deparment), for his advice on the geology of the Gifberg and Namaqua areas.
- Mandi Alblas and Shula Johnson, for technical assistance and coffee breaks.
- My husband, André Janse van Rensburg, for his patience, understanding, his keen interest in my work and many fun hours in the field. It is a great help and really means a lot if you share an interest for the great outdoors with your significant other!
- My wonderful friends and dedicated field assistants: Eloise Costandius, Cindy Shuttleworth, Christoff Truter, Jeannie Hayward, Anita Meyer, Johan du Plessis, Rebecca Fell, Nick Proust and Zoltán Korsós. Many thanks for making each field trip an exciting and memorable one. Without your help some of the work would have just not been possible!
- Rika du Plessis, Conservation Manager at Matjiesrivier Nature Reserve, for her assistance over the past couple of years, and the rustic, but lovely accommodation she made available at Matjiesrivier.

- All the farmers in the study area, for their hospitability and permission to work on their premises.
- CapeNature, for supplying the necessary permits.
- CEPF and the NRF, for financial support.
- The Zoology Department, for financial support to present my research at the 5th World Congress of Herpetology (June/July 2005) and the Herpetological Association of Africa (HAA) conference (November 2006).
- My family and all my other friends, for continuous encouragement and support during my studies.

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CHAPTER 1

GENERAL INTRODUCTION

1.1 THE CAPE FLORISTIC REGION

Situated at the southwestern tip of Africa, the Cape Floristic Region (CFR) is the smallest of six globally recognized floral kingdoms, comprising only 0.05% of land area, but containing nearly 3% of the world's plant species. It is globally recognized as a biodiversity hotspot (Myers *et al*. 2000), not only because of the high level of diversity and high degree of endemism in both plant (Goldblatt & Manning 2002) and animal groups (Branch 1988; Skelton *et al*. 1995; Picker & Samways 1996; Brooks *et al*. 2001), but also due to processes threatening this biodiversity (Rouget *et al*. 2003b). The number of endemic species in the different animal groups has resulted in the CFR being regarded as a "minor centre for endemism for all vertebrate groups" (Bigalke 1979). This is especially the case for the herpetofauna, with 24 (55%) of the 44 frog species, and 38 (26%) of the 145 reptile species occurring in the CFR being endemic. In the Western Cape alone, 22 (50%) of the 44 frog, and 21 (15%) of the 144 reptile species found in this province are endemic (Baard & De Villiers 2000). These numbers are, however, constantly changing with the discovery of new species.

The CFR has a wide range of habitats occurring within a small land area. A diverse topography - including the Cape Fold Mountains, lowlands, and coastal dunes - and the associated diverse climatic conditions resulted in a complex array of habitat types. Many of the processes that sustain endemism can occur in very small patches of remnant vegetation, giving rise to the unusual distribution of the CFR's biodiversity. Each fragment of natural habitat in the CFR can thus be considered as an area worthy of conservation action (CEPF

Ecosystem Profile: The Cape Floristic Region, South Africa, Final version, 11 Dec. 2001; Cowling *et al*. 2003).

1.2 SYSTEMATIC CONSERVATION PLANNING

Indiscriminate agricultural practice, urban development, invasive alien species, unsustainable use of resources, poor fire management, pollution, and climate change have been identified as major threats to biodiversity and have resulted in many species of the CFR now being endangered or close to extinction (Rebelo 1992a; Richardson, Van Wilgen & Higgins 1996; Baard *et al*. 1999; Rouget *et al*. 2003b; Latimer, Silander & Gelfand 2004). The CFR is therefore recognized as a global priority for conservation action (Myers *et al*. 2000; Cowling *et al*. 2003).

Previously, conservation areas had been chosen using an *ad hoc* approach and reserves were proclaimed in areas where opportunity of costs of conservation was low (Pressey 1994). Land areas with low potential for economic and political conflict, and high potential for recreation and tourism to biodiversity conservation, had thus been assigned to reserves (Pressey 1994; Rodrigues *et al*. 1999). In the CFR, this meant that rugged, inaccessible and infertile mountainous areas were selected for reserves and not productive and more densely populated lowland areas (Rebelo 1992b; Rouget, Richardson & Cowling 2003a).

Systematic conservation planning has three fundamental principles, namely representation, persistence and quantitative conservation target setting (GCBC: Biodiversity Spatial Plan Technical Report, Conservation Planning Unit, CapeNature, 17 January 2005). According to the representativeness concept, the entire range of biological and environmental variation within a given geographical area should be represented in a reserve (Margules & Usher 1981; Kirkpatrick 1983; Austin & Margules 1986; Mckenzie *et*

al. 1989). Reserves retaining only biodiversity patterns will not ensure long-term conservation of biodiversity (Cowling & Pressey 2001), and it is emphasized that the maintenance of natural processes be included as an important component of conservation area selection (Noss 1990; Balmford, Mace & Ginsberg 1998; Fairbanks & Benn 2000; Margules & Pressey 2000). For effective long-term conservation of biodiversity, it is thus necessary to conserve ecosystem processes that sustain ecosystem structure and function (Fairbanks & Benn 2000), and evolutionary processes that sustain lineages and generate diversity (Cowling *et al*. 1999).

1.3 THE CORRIDOR APPROACH

It is recognized that large parcels of habitat are essential for maintaining biodiversity and large-scale ecological processes (Noss 1996), but maintaining extensive areas of pristine habitat is becoming more difficult with the ever-increasing demands of the ever-growing human population. Every opportunity should therefore be taken to protect large areas of habitat.

In their ecosystem profile on the CFR (Final version, 11 Dec. 2001), the Critical Ecosystem Partnership Fund provides a practical and effective solution to conserving biodiversity, namely the corridor approach. Many existing protected areas are often too small and isolated to maintain viable ecosystems and evolutionary processes. In order to sustain these large-scale processes and ensure the maintenance of a high level of biodiversity, it is important that conservation efforts focus on linking major sites across wide geographic areas. These networks of protected areas and landscape management systems are called biodiversity corridors. The functional significance of corridors is to connect biodiversity areas through a patchwork of sustainable land uses. Even in the absence of large extensions of continuous natural habitat, these corridors will increase

mobility and genetic exchange among individuals of fauna and flora. Apart from promoting the immediate goals of regional-scale conservation based on individual protected areas, corridors also help maintain the ecosystem processes needed in order to sustain biodiversity into the future.

1.4 THE GREATER CEDERBERG BIODIVERSITY CORRIDOR (GCBC)

Following the Cape Action for People and the Environment (C.A.P.E.), CapeNature has been implementing three megareserves in the CFR (Cowling & Pressey 2003). These reserves are located in different biogeographic regions of the CFR (Cowling & Pressey 2003), incorporating areas of both public and private land (Boshoff, Cowling & Kerley 2000). These areas are capable of accommodating the ecological and evolutionary processes necessary to sustain biodiversity (Boshoff *et al*. 2000). One of these reserves, the Greater Cederberg Biodiversity Corridor (GCBC), covers an area of approximately 1.8 million ha (GCBC: Biodiversity Spatial Plan Technical Report, Conservation Planning Unit, CapeNature, 17 January 2005; www.cederbergcorridor.org.za). This reserve includes the Cederberg Mountains and the associated wilderness area, as well as the lowlands westwards in a corridor towards the coast. It incorporates the area from just north of Ceres in the south to just north of Nieuwoudtville in the north, and from Elandsbaai in the west to the Tanqua Karoo in the east (Fig. 1).

The geographical area where the GCBC was established represents a herpetological transition zone, and high species turnover is observed from north to south (Branch 1998). Several lowland and highland zones occur in parallel succession from west to east, with a diverse climatic system superimposed on this alternating landscape.

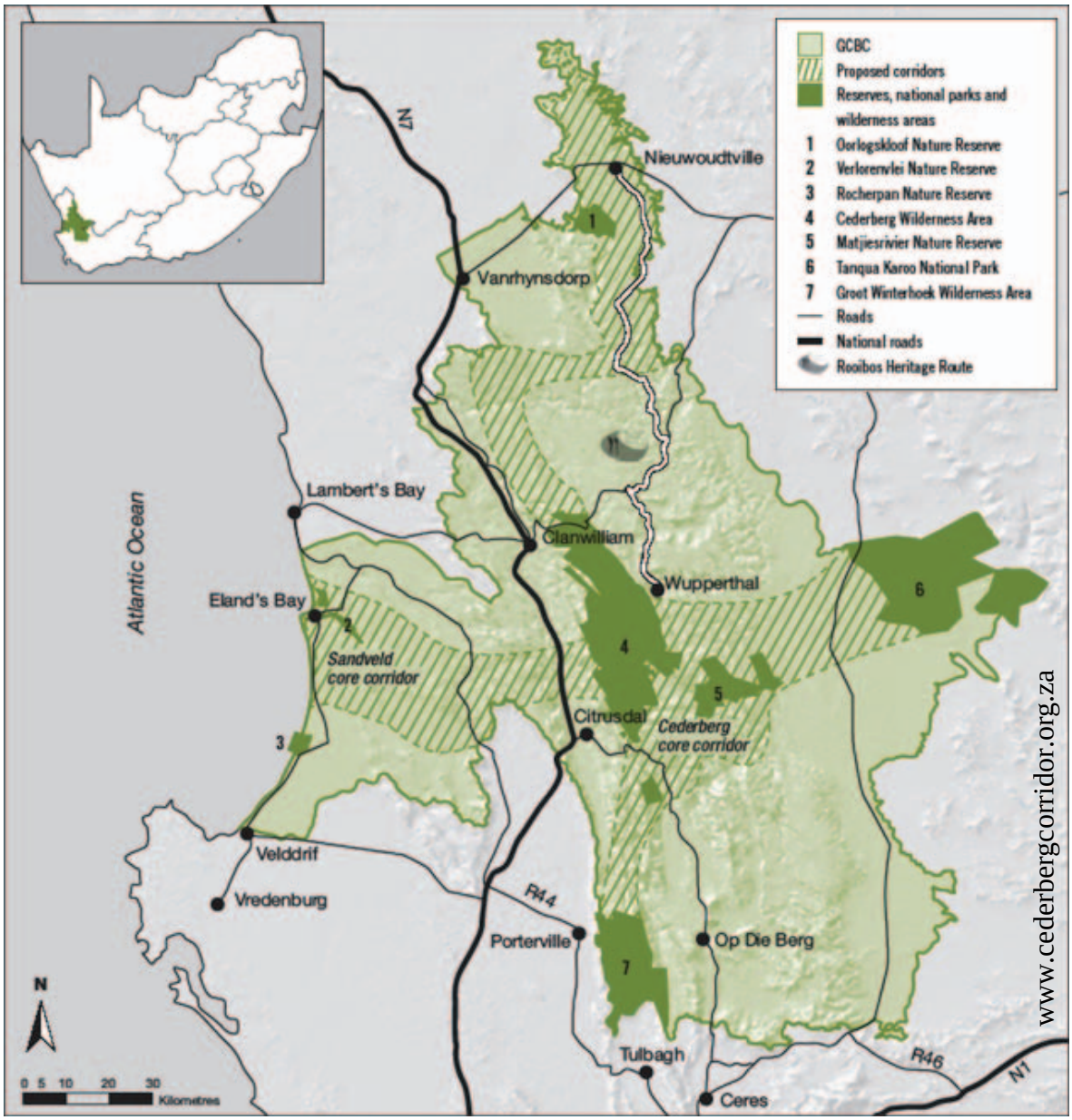

Figure 1. The Greater Cederberg Biodiversity Corridor.

1.5 MELANISTIC LIZARDS OF THE SOUTH-WESTERN CAPE

In the southwestern corner of southern Africa there is a distinct concentration of melanistic ectotherms, many displaying relictual distribution patterns (Mouton 1985, 1986a; Sirgel 1985; Endrödy-Younga 1988; Mouton & Oelofsen 1988; Mouton & Van Wyk 1995; Daniels, Mouton & Du Toit 2004). Being the result of a process (or processes) unique to the CFR, and because of the evolutionary and biological information they hold, these melanistic species are of considerable conservational and scientific importance. Melanistic lower vertebrates occurring in the south-west comprise at least eight melanistic cordylid lizard species.

The Black Girdled lizard, *Cordylus niger* (Fig. 2a), is found on the Cape Peninsula (from the northern slopes of Table Mountain to Cape Point), as well as in the Saldanha-Langebaan area (including Jutten Island) (FitzSimons 1943; Mouton 1985, 1986a, 1987).

The melanistic morph of the polymorphic Karoo Girdled Lizard, *Cordylus polyzonus* (Fig. 2d), occurs in isolated populations along the west coast, from the Orange River to the Saldanha-Langebaan area (FitzSimons 1943; Mouton 1985, 1986a, 1987). There are also reports of two small melanistic populations of the latter occurring in the central part of South Africa (Mouton 1986a). Due to the isolated nature of their distribution, as well as deficient distribution data, the inland melanistic populations of *C. polyzonus* were not included in this study.

The *oelofseni*-complex consists of three species, namely *Cordylus oelofseni*, and two undescribed species (Daniels *et al*. 2004) (Fig. 2b). For the purpose of this study, they will be referred to as *Cordylus oelofseni* (O), *Cordylus oelofseni* (P) and *Cordylus oelofseni* (H). *Cordylus oelofseni* (O) occurs as several isolated populations in the Olifantsrivier Mountains (Mouton 1985, 1986a, 1987; Mouton & Oelofsen 1988; Mouton & Van Wyk 1990; Daniels *et al*. 2004). *Cordylus oelofseni* (P) occurs on the Piketberg Mountains,

whereas *C. oelofseni* (H) is found on the Hottentots Holland Mountains in the south (Daniels *et al*. 2004).

Peers' Girdled Lizard, *Cordylus peersi* (Fig. 2c), is found in the Namaqualand Highlands of the Northern Cape (FitzSimons 1943), an area that is characterized by large gneiss outcrops in a very hilly area.

The Dwarf Crag Lizard or Cloud Lizard, *Pseudocordylus nebulosus* (Fig. 2e), has a very limited distribution and is restricted to only a very small area in the Hottentots Holland Mountains (Mouton & Van Wyk 1995; Costandius, Mouton & Boucher 2006).

The Graceful Crag Lizard, *Pseudocordylus capensis* (Fig. 2f), occurs from Nieuwoudtville in the north along the Matsikamma and Cederberg Mountains southwards, and eastwards to the Kamanassie Mountains (FitzSimons 1943; Mouton 1985; Herselman, Mouton & Van Wyk 1992; Bauer & Branch 1995).

Several hypotheses have been listed to explain melanism in ectotherms, including thermal consequences, protection from ultraviolet (UV) light, resistance or response to injury, camouflage and crypsis, aposematism, sexual selection, and non-selective physiological by-production (Majerus 1998), but these have mainly been investigated for insects. Cryptic colouration and increased efficiency for heat-absorption in cooler environments are, however, probably the two main hypotheses that have been put forward for the occurrence of melanism in natural populations of reptiles (Norris 1967; Porter 1972; Endler 1978; Hoppe 1979; Pearse & Pogson 2000; White, Powell & Censky 2002; Clusella Trullas, Van Wyk & Spotila 2007a).

Most melanistic cordylid species occur as small isolated populations at either coastal or montane localities (see Branch (1998) and Chapter 3 for distribution maps). Coastal melanistic cordylid populations are restricted to localities along the coast associated with zones of upwelling of cold water in the Atlantic Ocean (Badenhorst 1990; Badenhorst,

Figure 2. Melanistic cordylids of southern Africa: a) *Cordylus niger*; b) *C. oelofseni*; c) *C. peersi*; d) *C. polyzonus*; e) *Pseudocordylus nebulosus*; and f) *P. capensis*.

Mouton & Van Wyk 1992; Chapter 2). Montane melanistic cordylids occur on the western parts of the Cape Fold Mountains (CFM), where there is a high incidence of orographic fog and cloud cover (Badenhorst 1990; Badenhorst *et al*. 1992; Chapter 2). Mouton & Oelofsen (1988) suggested that the concentration of melanistic taxa in the southwestern corner of southern Africa, and the occurrence of these populations in insular and peninsular areas along the coast and at higher altitudes inland, are indicative that melanism is a result of certain climatic pressures rather than biotic or other factors.

Of the eight melanistic cordylid species occurring in the southwest, *Pseudocordylus capensis* has by far the largest distribution range, and is found to occur in isolated populations in both cool highland and warm lowland situations (Herselman, Mouton & Van Wyk 1992; Branch 1998). The only other melanistic cordylid not restricted to coastal or montane areas is *Cordylus peersi*, which also has a relatively wide distribution in Namaqualand (Branch 1998; Chapter 3, Chapter 4).

It is generally accepted that organisms occur in environmental conditions similar to those they have adapted to during their speciation (Vrba 1985; Endrödy-Younga 1988). All indications are that the present melanistic ectotherm populations in the Western Cape are relicts of once larger populations of cold-adapted forms (Sirgel 1985; Endrödy-Younga 1988; Mouton & Oelofsen 1988; Brody, Mouton & Grant 1993; Daniels *et al*. 2004; Chapter 2). These melanistic populations originated some time in the past during a period of limited solar radiation unique to the southwestern tip of Africa (Mouton & Oelofsen 1988; Daniels *et al*. 2004). During climatic changes along the southwestern coastal areas, these populations then fragmented, remaining only in suitable cooler enclaves that act as refugia for these cold-adapted forms (Mouton & Oelofsen 1988; Daniels *et al*. 2004). Being small, these relictual populations are thus more likely to speciate than large populations. Molecular data presented by Daniels *et al*. (2004) suggest that melanism in

the *cordylus-niger-oelofseni* clade evolved during the Miocene epoch (17-15 MYA). Further studies are, however, needed to investigate if melanism evolved during the same period in other ectotherm taxa.

To date, studies have mainly reported on the thermoregulatory advantages of having a dark skin (Atsatt 1939; Cole 1943; Fitch 1955; Bartlett & Gates 1967; Norris 1967; Gibson & Falls 1979; Clusella Trullas *et al*. 2007a). A black body would emit and absorb radiant energy more efficiently than a lighter coloured animal (Jones & Childers 2001). A dark skin may thus have thermoregulatory advantages in cold environments, which will allow melanistic species to have a large distribution during glacial periods (Norris 1967; Porter 1967; Heatwole 1976; Pearson 1977; Rice & Bradshaw 1980; Clusella Trullas *et al*. 2007a; Clusella, Van Wyk & Spotila 2009). During interglacial periods, the opposite may be true, and melanism may prove to be a constraint (Clusella Trullas *et al*. 2007a), resulting in the contraction of the distribution ranges of melanistic species with ameliorating climatic conditions.

The extensive range of *P. capensis*, relative to other melanistic cordylids, suggests that this species has a broader tolerance range for warm temperatures than the other species. Understanding those characteristics increasing the temperature tolerance range of melanistic cordylids is important for deriving specific conservation targets for these species, especially for lowland populations such as those in the greater Cederberg area.

1.6 Significance of the Study and Key Aspects

To evaluate the significance of the Greater Cederberg Biodiversity Corridor initiative for the effective conservation of herpetofauna in the Cape Floristic Region, a collaborative study of the herpetofauna of the GCBC (*Effective Conservation of Amphibians and Reptiles of the Greater Cederberg Biodiversity Corridor - SCARCE*) was initiated in 2004,

with the University of Stellenbosch and CapeNature as the two main partners. One of the herpetological conservation targets identified for the GCBC was an understanding of the ecology of melanistic cordylid populations with particular reference to global environmental change.

Pseudocordylus capensis and *Cordylus peersi* are two melanistic species occurring in lowland areas, the other six species being restricted to coastal areas or the mistbelt of the western Cape Fold Mountains. The previously proposed association of melanistic populations with cool climates (Badenhorst 1990; Badenhorst *et al*.1992) was based on an incomplete data set. A detailed analysis of the geographical distribution of melanistic cordylid species, involving all species, and a search for climatic correlates explaining the observed patterns of distribution, was required as a starting point. Such an analysis characterized the climatic variables associated with the distribution of melanistic cordylid species, and might prove to be an useful in making predictions on potential range contractions or expansions that may occur in the future due to climate change.

Distinct differences in the extent of the ranges of the eight melanistic cordylid species, suggested that the species might vary considerably in the degree to which melanism might be a constraint in warm climates. Lizards often display physiological, morphological or behavioural adaptations to a specific (micro)habitat (Vanhooydonck, Van Damme & Aerts 2000). Identifying those phenotypic attributes responsible for differences in response to the limiting effects of climate was the logical next step in the understanding of the ecology of melanistic cordylids. This study was the first step in that direction, and investigated the morphological aspects of melanistic cordylids. It was expected that certain morphological trade-offs were responsible for increasing the performance breadth of some of the melanistic species, and that these trade-offs compromised other daily activities such

as foraging behaviour, social structure (including space-use, territoriality, and mating system), and predator-prey relationships.

The GCBC is home to two of the eight melanistic cordylid species found in the southwestern corner of southern Africa. Isolated populations of Oelofsen's girdled lizard, *Cordylus oelofseni*, occur in the southern part of the GCBC. The graceful crag lizard, *P. capensis*, is one of the two melanistic cordylids species not restricted to the extreme southwestern Cape, and occurs in isolated populations throughout the corridor, except in the western coastal lowlands and the Tankwa Karoo. In light of the presumed constraints of melanism in warm climates, the future of many isolated populations of *P. capensis* in the GCBC is a matter of concern, particularly with respect to global warming.

To summarize, the overall goal of this study was to investigate what morphological trade-offs were enabling certain melanistic cordylid species to survive in warm climates while others cannot, and to obtain information that would facilitate the effective conservation of melanistic cordylid species/populations in the GCBC. The specific objectives of the study were:

1. To conduct a geographical analysis in an attempt to characterize the climate regime associated with the distribution of melanistic cordylids;
2. To identify morphological and habitat characteristics of melanistic cordylids, and how they relate to each other. In other words, what is the relationship between morphology and habitat and how this increase the performance breadth of melanistic cordylids occurring in warm climates (i.e. the ability of these lizards to make effective use of the range of microclimates available to them);
3. To investigate the impact of parameters increasing performance breadth on other life functions such as: (a) predator- prey relationships; and (b) spacing patterns and foraging behaviour;

The data obtained during this study would provide a framework for future studies on melanism in cordylids, and also contribute to the conservation of the South African reptile diversity. The end goal will be to have a complete understanding of melanism in terms of lizard performance and the influence thereof on life functions for all melanistic cordylids. This will give us insight into how the different species function in their specific habitats and how they are likely to cope with climate change.

Please note that while the chapters follow on the previous one, each chapter has also been written in such a manner that it can be read as a free-standing article, and some information overlap among chapters was therefore unavoidable.

CHAPTER 2

WHY CORDYLID LIZARDS ARE BLACK AT THE SOUTH-WESTERN TIP OF AFRICA*

2.1 INTRODUCTION

Many reptile clades contain melanistic species or species with melanistic morphs, with individuals having a dark pigmentation and appearing almost black in colour (True 2003). Numerous functions have been advanced for melanism, including a role in thermoregulation (e.g. Kettlewell 1973; Kingsolver & Wiernaz 1991; Clusella Trullas, Van Wyk & Spotila 2007), protection from ultraviolet (UV) radiation (e.g. Setlow *et al*. 1993; Gunn 1998; Callaghan *et al*. 2004; Calbó, Pagès & González 2005), cryptic coloration (e.g. Kettlewell 1973; Endler 1984), aposematism (e.g. Turner 1977), and intraspecific communication (sexual selection) (e.g. Wiernasz 1989). The role of melanism in thermoregulation has been well-studied (see Clusella Trullas *et al*. 2007a for a review) and the thermal melanism hypothesis has been formulated. Melanistic individuals should under the same environmental conditions heat faster and reach higher equilibrium temperatures than lighter coloured ones of similar body size (Gates 1980). It follows that, under conditions of low ambient temperature, melanistic individuals will be able to maintain higher body temperatures and have longer periods of activity, putting them at an advantage over non-melanistic individuals.

The thermal melanism hypothesis is underlain by four key assumptions: 1) melanistic species occur in cooler environments than non-melanistic species; 2) melanism leads to greater overall fitness in cool environments; 3) there is a trade-off between melanism and body size; 4) colour, behaviour and physiology are co-adapted (Clusella Trullas *et al*. 2007a). The assumption that melanistic species should be restricted to cool environments is not only based on the potential advantage of increased absorption of solar radiation in cool climates,

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but also on the possibility of overheating in warm environments, should the limits of behavioural compensation be exceeded (Clusella Trullas *et al*. 2007a).

The Cordylidae is a family of lizards endemic to Africa. The majority of species are rock-dwelling and three of the four genera currently recognized, are viviparous (Mouton & Van Wyk 1997; Branch 1998). Based on an evolutionary shift from an active foraging mode to a sit-and-wait one, from a ground-dwelling lifestyle to a rock-dwelling one, and eventually from oviparity to viviparity, Mouton & Van Wyk (1997) concluded that the family had a cold climate origin. What makes cordylids unique among South African lizards is the high incidence of melanism and the fact that these melanistic species are restricted to the south-western tip of the continent (Fig. 1). Here, at least eight melanistic species occur in habitats ranging from sea level to mountain top (Mouton 1985, 1986a; Mouton & Oelofsen 1988; Mouton & Van Wyk 1995; Daniels, Mouton & Du Toit 2004). A preliminary phylogeny for the family (Frost *et al*. 2001), as well as unpublished results of other molecular analyses (J. Melville pers. comm.; E. Stanley pers. comm.), indicated that melanism evolved several times in the family.

Several authors have suggested that melanism in cordylid lizards has a thermoregulatory function and that it has evolved in response to cool climatic conditions associated with the cold Benguela Current (Mouton 1985, 1986a; Mouton & Oelofsen 1988; Badenhorst 1990; Badenhorst *et al*. 1992; Daniels *et al*. 2004). The aim of this study was to determine the climatic conditions with which melanistic cordylid species are presently associated. In line with the thermal melanism hypothesis, I predicted that melanistic cordylids will be restricted to relatively cool environments.

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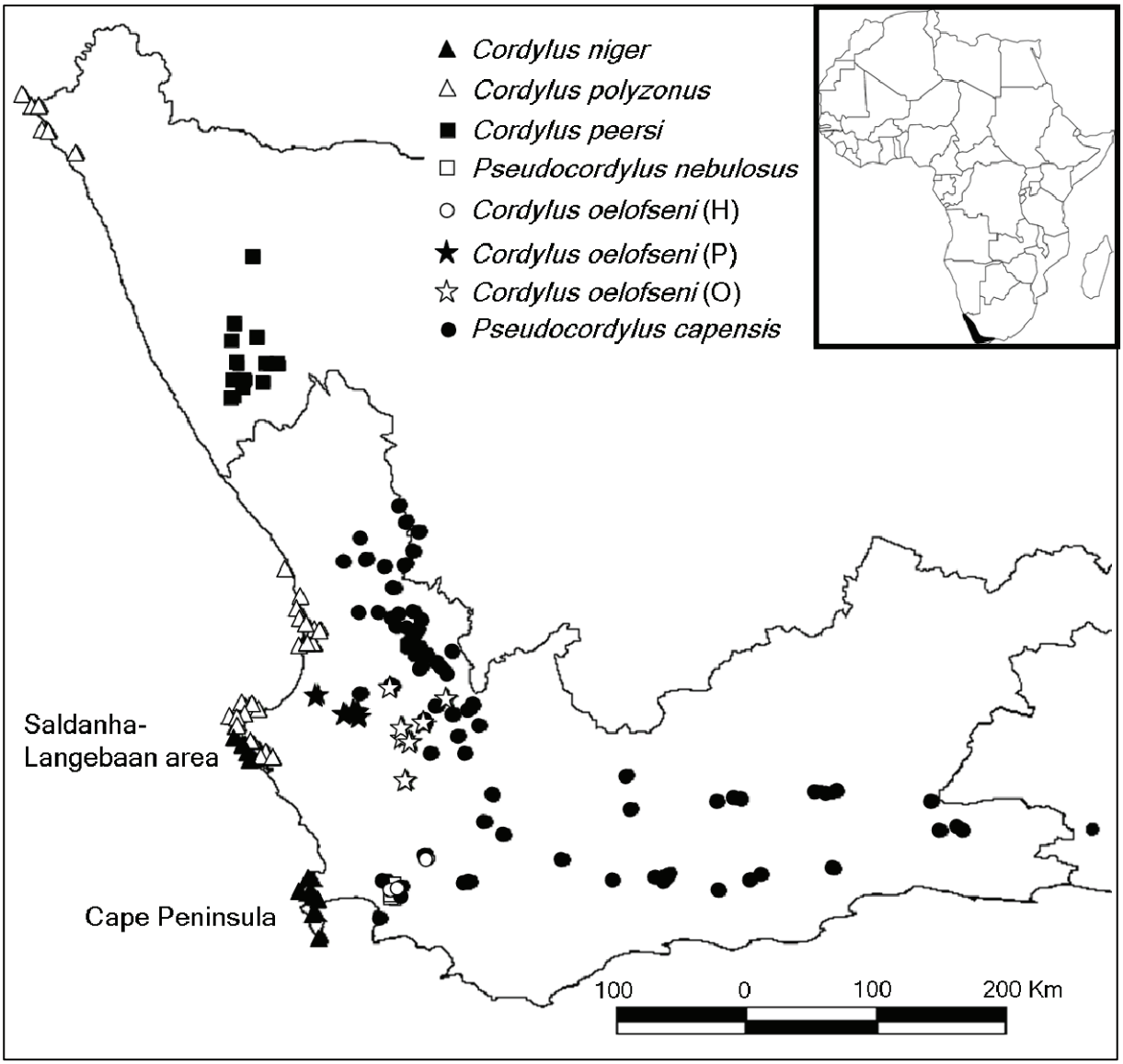

Figure 1. Distribution of the eight melanistic cordylid lizard species occurring at the south-western tip of Africa.

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2.2 MATERIALS AND METHODS

Distributional data for the eight melanistic cordylid taxa occurring in the south-western parts of South Africa were obtained from the CapeNature State of Biodiversity database, which includes records from all major South African collections. There is a distinct possibility that two populations of *Cordylus oelofseni* may be described as new species (see Daniels *et al*. 2004), and the three populations in the complex are therefore considered separately and referred to as *C. oelofseni* (O), *C. oelofseni* (H) and *C. oelofseni* (P). Using GIS, altitude, as well as the monthly means for the following climatic variables was compiled for each locality where melanistic cordylids have been recorded: maximum temperature, minimum temperature, solar radiation, rainfall, relative humidity and potential evaporation. From these, mean annual values and the means of the five hottest months (November–March) were calculated for each locality. In addition, the average number of days per year with fog, and average annual cloud cover (measured in eights) were also determined.

To characterize the climatic variables associated with the distribution of melanistic cordylid species, a Principal Component Analysis (PCA) was performed using SYNTAX 2000 (Podani 2001). After outliers were identified and masked-out, another PCA was performed on the reduced data set. In a third PCA, only the data for the five hottest months were used.

2.3 RESULTS

2.3.1 Altitude

The recorded altitudinal ranges for the eight melanistic taxa are summarized in Table 1. With the exception of *Pseudocordylus capensis*, inland populations of all melanistic species occur at relatively high altitudes, nowhere below 320 m a.s.l. *Pseudocordylus capensis* was recorded from altitudes as low as 50 m a.s.l. to over 2000 m a.s.l.

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Table 1. Summary of the altitudes and the mean annual climatic data at which melanistic cordylid species occur.

	Cordylus niger	*Cordylus oelofseni* (H)	*Cordylus oelofseni*(O)	*Cordylus oelofseni* (P)	*Cordylus peersi*	*Cordylus polyzonus*	*Pseudocordylus capensis*	*Pseudocordylus nebulosus*
Altitude (m)								
Average ± SE	193.62 ± 39.62	1148.0 ± 114.3	787.38 ± 141.17	625.5 ± 113.91	742.42 ± 91.3	82.96 ± 8.62	1270.53 ± 49.05	1075.5 ± 2.02
Range	0.0 - 587.0	880.0 - 1561.0	377.0 - 1578.0	321.0 - 868.0	341.0 - 1218.0	4.0 - 294.0	53.0 - 2098.0	1072.0 - 1079.0
Maximum temperature (°C)								
Average ± SE	20.15 ± 0.23	15.35 ± 0.42	21.79 ± 0.54	21.31 ± 0.65	22.49 ± 0.35	22.37 ± 0.15	19.4 ± 0.14	15.46 ± 0.45
Range	13.0 - 27.0	10.0 - 21.0	10.0 - 31.0	14.0 - 29.0	14.0 - 29.0	16.0 - 32.0	8.0 - 33.0	11.0 - 20.0
Minimum temperature (°C)								
Average ± SE	10.81 ± 0.16	6.25 ± 0.3	8.72 ± 0.37	9.54 ± 0.46	9.0 ± 0.28	11.24 ± 0.11	6.62 ± 0.1	6.67 ± 0.29
Range	7.0 - 15.0	2.0 - 10.0	1.0 - 15.0	4.0 -15.0	3.0 - 15.0	7.0 - 16.0	-2.0 - 16.0	4.0 - 10.0
Solar radiation ($MJ.m^{-2}$.day-1)								
Average ± SE	18.96 ± 0.38	18.22 ± 0.85	22.97 ± 0.83	21.74 ± 1.06	23.64 ± 0.59	20.96 ± 0.25	22.56 ± 0.22	17.75 ± 0.89
Range	9.5 - 28.6	9.1 - 29.6	10.2 - 34.7	11.2 - 31.6	13.0 - 34.3	11.3 - 34.4	9.1 - 38.1	9.3 - 26.6
Rainfall (mm)								
Average ± SE	55.29 ± 3.32	136.87 ± 12.67	35.45 ± 2.74	40.04 ± 5.12	11.66 ± 0.91	14.61 ± 0.58	38.62 ± 1.2	140.46 ± 12.92
Range	1.0 - 211.0	10.0 - 330.0	3.0 - 100.0	2.0 - 119.0	0.0 - 37.0	0.0 - 54.0	0.0 - 412.0	37.0 - 292.0
Relative humidity (%)								
Average ± SE	73.50 ± 0.16	73.12 ± 0.43	64.83 ± 0.34	67.67 ± 0.38	63.96 ± 0.17	69.57 ± 3.84	65.03 ± 0.13	74.29 ± 0.4
Range	68.0 - 81.0	65.0 - 78.0	60.0 - 73.0	64.0 - 73.0	59.0 - 71.0	60.0 - 76.0	55.0 -81.0	70.0 - 79.0
Potential evaporation (mm)								
Average ± SE	157.12 ± 5.15	72.8 ± 4.15	176.06 ± 9.33	172.75 ± 12.75	199.65 ± 7.35	190.15 ± 3.59	150.54 ± 2.18	71.17 ± 4.12
Range	57.0 - 331.0	21.0 - 170.0	51.0 - 339.0	52.0 - 325.0	79.0 - 364.0	60.0 - 393.0	3.0 - 366.0	26.0 - 133.0
Fog (days)								
Average ± SE	49.81 ± 6.63	17.45 ± 0.51	31.15 ± 1.31	43.81 ± 1.84	31.57 ± 2.45	67.53 ± 3.31	24.14 ± 0.63	17.96 ± 0.0
Range	13.89 - 88.74	15.41 - 17.96	23.22 - 33-7	41.89 - 49.32	6.82 - 38.88	30.93 - 107.58	4.42 - 45.45	17.96
Cloud cover (eights)								
Average ± SE	3.05 ± 0.03	2.89 ± 0.02	2.88 ± 0.03	2.9 ± 0.01	2.22 ± 0.02	2.72 ± 0.04	2.96 ± 0.04	2.87 ± 0.0
Range	2.97 - 3.41	2.87 - 2.96	2.75 - 2.98	2.87 - 2.92	2.01 - 2.31	2.01 - 3.0	2.03 - 3.96	2.87

2.3.2 Climate

The means of the climatic variables describing the range of each melanistic cordylid species are summarized in Table 1 and 2. In the first PCA, the first two axes accounted for 77.83% of the variation (Fig. 2; Table 3), indicating that the selected climatic variables structured the data well. Strong correlations between cloud and rain, and between mean maximum temperature and potential evaporation were evident. Similar results were obtained when only data for the five hottest months were used in the analysis and the first two axes accounted for 79% of the variation. After removal of outliers, the first two axes accounted for 78% of the variation with the same correlations among the variables observed.

In all analyses, *Pseudocordylus capensis*, being the species with the widest distribution, also occupied the largest portion of ordination space. The other melanistic species (all having limited distributions) were shown to occupy restricted climatic niches (Fig. 2). The coastal melanistic populations of *Cordylus niger* and *Cordylus polyzonus* were found to be associated with a high incidence of fog along the west coast (Fig. 3, 4). The *C. niger* population on the Cape Peninsula is also influenced by high humidity, cloud cover and rainfall. Two of the montane species, *Pseudocordylus nebulosus* and *C. oelofseni* (H), are closely associated with high cloud cover and rainfall (Fig. 2, 5). *Cordylus oelofseni* (O), *C. oelofseni* (P), *Cordylus peersi* and the Lambert's Bay melanistic population of *C. polyzonus*, which occur at lower altitudes than the other montane species, are associated with higher mean temperatures than the other melanistic species (Fig. 2). Although *C. peersi* is associated with relatively high mean temperatures and high levels of solar radiation, the species is restricted to a relatively cool enclave in the Namaqualand region (Fig. 6). *Pseudocordylus capensis* populations occurring above 1000 m a.s.l. are closely associated with high levels of cloud cover, and rainfall, while populations below 1000 m a..s.l. are more closely associated with high temperatures and high levels of solar radiation (Fig. 2 and 6).

Table 2. Summary of the altitudes and the mean climatic data for the five hottest months (November – March) at which melanistic cordylid species occur.

	Cordylus niger	*Cordylus oelofseni* **(H)**	*Cordylus oelofseni***(O)**	*Cordylus oelofseni* **(P)**	*Cordylus peersi*	*Cordylus polyzonus*	*Pseudocordylus capensis*	*Pseudocordylus nebulosus*
Altitude (m)								
Average ± SE	193.62 ± 39.62	1148.0 ± 114.3	787.38 ± 141.17	625.5 ± 113.91	742.42 ± 91.3	82.96 ± 8.62	1270.53 ± 49.05	1075.5 ± 2.02
Range	0.0 - 587.0	880.0 - 1561.0	377.0 - 1578.0	321.0 - 868.0	341.0 - 1218.0	4.0 - 294.0	53.0 - 2098.0	1072.0 - 1079.0
Maximum temperature (°C)								
Average ± SE	23.67 ± 0.15	18.68 ± 0.25	26.7 ± 0.43	25.75 ± 0.38	26.48 ± 0.21	25.68 ± 0.12	24.06 ± 0.14	18.7 ± 0.23
Range	19.0 - 27.0	16.0 - 21.0	21.0 - 31.0	22.0 - 29.0	22.0 - 29.0	22.0 - 32.0	15.0 - 33.0	17.0 - 20.0
Minimum temperature (°C)								
Average ± SE	13.42 ± 0.12	8.32 ± 0.29	12.05 ± 0.32	12.6 ± 0.35	12.33 ± 0.2	14.08 ± 0.05	9.63 ± 0.1	8.6 ± 0.23
Range	10.0 - 15.0	5.0 - 10.0	7.0 - 15.0	9.0 - 15.0	9.0 - 15.0	12.0 - 16.0	4.0 - 16.0	7.0 - 10.0
Solar radiation (MJ.m^{-2}.day-1)								
Average ± SE	24.95 ± 0.21	24.78 ± 0.59	30.98 ± 0.51	29.03 ± 0.61	30.29 ± 0.39	26.88 ± 0.19	30.58 ± 0.17	23.93 ± 0.56
Range	20.30 - 28.60	19.5 - 29.6	23.9 - 34.7	23.7 - 31.6	23.1 - 34.3	20.8 - 34.4	17.9 - 38.1	19.7 - 26.6
Rainfall (mm)								
Average ± SE	18.43 ± 1.38	52.92 ± 4.72	10.6 ± 0.67	10.65 ± 1.31	1.62 ± 0.2	2.93 ± 0.14	18.4 ± 0.9	54.0 ± 2.93
Range	1.0 - 49.0	10.0 - 90.0	3.0 - 19.0	2.0 - 23.0	0.0 - 5.0	0.0 - 10.0	0.0 - 143.0	37.0 - 78.0
Relative humidity (%)								
Average ± SE	71.7 ± 0.19	70.2 ± 0.46	62.05 ± 0.22	65.3 ± 0.15	63.43 ± 0.27	69.02 ± 3.79	62.21 ± 0.16	71.7 ± 0.23
Range	68.0 - 75.0	65.0 - 73.0	60.0 - 65.0	64.0 - 67.0	60.0 - 71.0	60.0 - 74.0	55.0 - 77.0	70.0 - 73.0
Potential evaporation (mm)								
Average ± SE	241.69 ± 4.20	101.48 ± 5.71	271.05 ± 6.74	265.15 ± 8.29	289.43 ± 6.05	285.0 ± 2.37	221.82 ± 2.99	96.8 ± 5.4
Range	157.0 -331.0	57.0 - 170.0	189.0 - 339.0	206.0 - 325.0	202.0 - 364.0	223.0 -393.0	3.0 - 366.0	60.0 - 133.0

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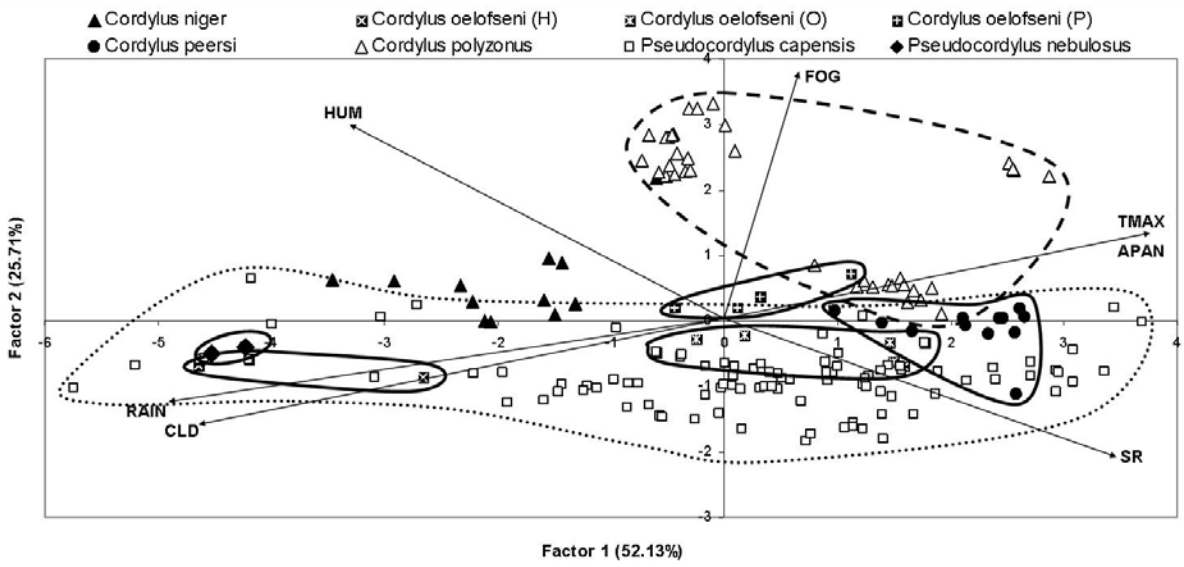

Figure 2. First and second axes for the first PCA. Climatic variables are indicated by the arrows.

Table 3. PCA on mean annual climatic data.

	Component loadings	
Variable	1	2
Fog	0.144	0.921
Cloud	-0.464	-0.162
Tmax	0.823	0.282
Radiation	0.836	-0.529
Rainfall	-0.805	-0.211
Humidity	-0.736	0.642
APAN	0.920	0.330
Eigenvalue	3.65	1.80
% variance explained	52.13	25.71

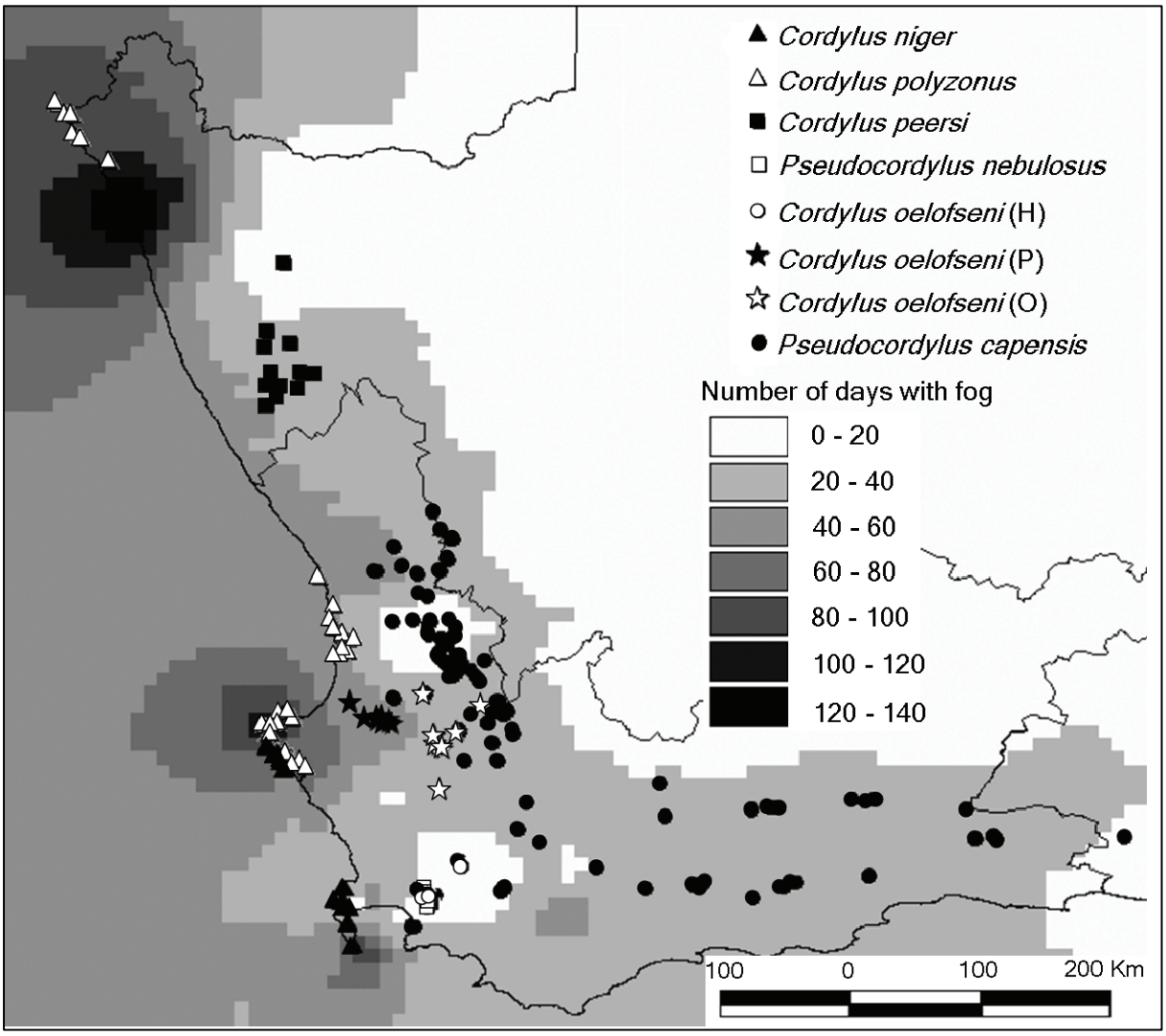

Figure 3. Map showing the mean annual days with fog per locality.

Figure 4. The west coast of South Africa has a high incidence of coastal fog.

(a)

(b)

Figure 5. The Cape Fold Mountains experience a high occurrence of orographic cloud cover (a), especially in the Landdroskop area (b).

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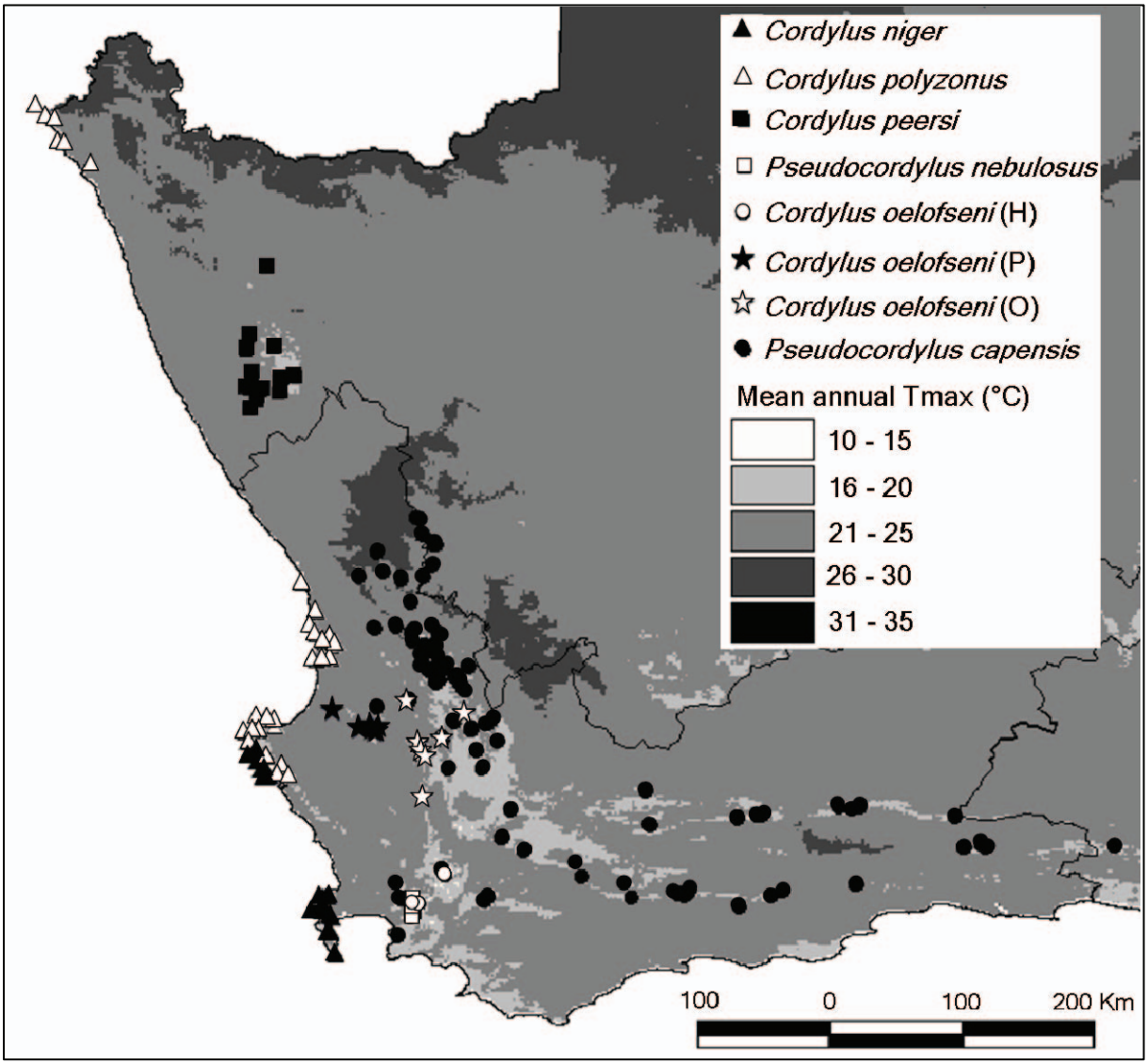

Figure 6. Map showing mean annual maximum temperatures.

2.4 DISCUSSION

The results of my study show that there is no single set of climatic conditions that describes the geographical distribution of melanistic cordylid lizards in south-western South Africa. In line with the assumptions of the thermal melanism hypothesis, several melanistic cordylid taxa, however, distinctly occur in association with a high incidence of fog or cloud cover and relatively cool climatic conditions. This is best illustrated along the west coast, where in the Saldanha-Langebaan area of high fog incidence (Fig. 3), two melanistic cordylid taxa co-occur (Cordes & Mouton 1996). Further north, at Alexander Bay, another main high fog incidence area, a melanistic *C. polyzonus* population occurs (Fig. 3). In the southern Cape Peninsula, a third area of high fog incidence, *C. niger* is particularly abundant. Fog along the west coast is the result of the north-flowing cold Benguela Current that brings cool water right against the west coast of southern African (Schulze 1965; Brown & Jarman 1978). Associated with this cold current, are semi-permanent zones of upwelling of even colder water, especially during the summer months (Hart & Currie 1960; Schulze 1965; Andrews & Hutchings 1980; Taunton-Clark 1982). When cold offshore air meets the warm air from the mainland along these upwelling zones, it results in thick fog that can last for several hours or even days (Barry & Chorley 1982).

Inland, the Landdroskop locality in the Hottentots Holland Mountains deserves specific mention. No less than three melanistic cordylids co-occur at this locality, one of them (*P. nebulosus*) being restricted to this site (Costandius, Mouton & Boucher 2006). This locality experiences an exceptionally high incidence of orographic fog during summer months when southwesterly to southeasterly winds are blowing, and, in addition, lies within the general area with the highest annual rainfall in South Africa (Badenhorst 1990). Sirgel (1985), for example, reported that cloud cover is present for at least part of the day on more than 200 days per year at this locality. Orographic fog at mountain tops during summer months is a

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common phenomenon along the Cape Fold Mountains (Heydorn & Tinley 1980), but we suspect that the resolution of our GIS analysis was not fine enough to capture localized occurrences of orographic fog and associated cooler climatic conditions. The results of our analysis may therefore be an underestimation of the climatic conditions with which many inland melanistic populations are associated.

Pseudocordylus capensis is the only melanistic cordylid, which is seemingly not confined to cool environments. In the southern half of its range, it typically occurs at mountain tops and under similar climatic conditions where other melanistic cordylids would be found (Fig. 6). In the northern half of its range, it is, however, often found in warm lowland environments, but always in association with a very particular habitat type. It typically occurs along river courses where there are high rock formations on the sides, and is particularly common at waterfalls (Chapter 3). When occurring away from river courses, it is always associated with huge boulders or cliff faces (Chapter 3). These habitats have a range of qualities, among others, ample shade, an altitudinal range of perching options and the presence of water, all of which could allow for effective thermoregulation by this melanistic species during the hot summer months (Chapter 3, 4). *Cordylus peersi*, the northernmost inland melanistic cordylid, is like *P. capensis*, typically associated with huge boulders, especially at lower altitudes (Fell 2005). In contrast to other melanistic cordylids, both *P. capensis* and *C. peersi* have long limbs, allowing them to scale vertical surfaces and giving them greater flexibility in habitat use (Chapter 3).

A molecular analysis of phylogenetic relationships in the *cordylus-niger-oelofseni* complex (Daniels *et al*. 2004) provided evidence that melanism in this complex evolved during Miocene times, in other words at the time of origin of the Cold Benguela Current (Tankard & Rogers 1978; Siesser 1980; Hendey 1983). The present fragmented ranges of *C. niger* and *C. oelofseni* suggest that the climatic conditions with which melanism is associated

today, sometime in the past occurred widely in south-western South Africa (Mouton & Oelofsen 1988; Daniels *et al*. 2004). Daniels *et al*. (2004) suggested that melanism in other cordylids also evolved during this time. After amelioration of climates, the melanistic forms managed to survive, because cool refugia along the west coast and in the mountains were always available.

Of the seven lizard families presently represented in south-western South Africa (Branch 1998), melanism is confined to the Cordylidae. The absence of melanistic representatives from other families can be the result of one or a combination of factors. Firstly, there is a strong possibility that the adverse climatic conditions that resulted in the evolution of melanism in cordylids, would have excluded oviparous forms from the south-western coastal areas. A high incidence of fog and cloud cover (Mouton & Oelofsen 1988) would not have been conducive to egg development, and reproductive success would have been compromised.

Secondly, the energy demands of an active foraging mode may have excluded actively foraging taxa from the south-western coastal lowlands during the assumed period of adverse climatic conditions when melanism evolved in cordylids. It is well known that the energetic costs of foraging are higher for active foragers because, in terrestrial vertebrates, movements results in a twofold to 10-fold increase in energy metabolism (Schmidt-Nielsen 1972; Taylor 1973; Anderson & Karasov 1981). In contrast to cordylids, which are all sit-and-wait foragers (Cooper, Whiting & Van Wyk 1997; Mouton & Van Wyk 1997), the majority of lacertids (Cooper & Whiting 1999) and all scincids and gerrhosaurids (Mouton & Van Wyk 1997) are active foragers. Given the evolutionary conservativeness of foraging mode among lizard clades (Cooper 1995), the overall energy requirements of active foraging may have excluded most of these forms from the south-western coastal areas during the assumed period of adverse climatic conditions.

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Thirdly, the ability of chameleons, agamas and geckos to physiologically regulate body colour according to environmental conditions probably would have made permanent darkening of the skin unnecessary. Finally, besides the constraints of an oviparous reproductive mode and an active foraging mode in cool environments, a ground-dwelling lifestyle, as is found in most lacertids, scincids and gerrhosaurids (Mouton & Van Wyk 1997) would have provided these taxa with greater vagility than rock-dwelling taxa have. The latter would have been particularly prone to give rise to geographical isolates in which melanism could have evolved relatively quickly.

In summary, the viviparous reproductive mode, sit-and-wait foraging strategy, rock-dwelling lifestyle and inability to regulate body colour made cordylids perfect candidates for evolving melanism during a prolonged period of high fog incidence and cloud cover. Today, other viviparous clades occurring in these south-western coastal areas include the chameleon genus *Bradypodion* and several scincid genera. The evolution of viviparity in *Bradypodion* apparently coincided with the origin of the cold Benguela Current during the Miocene (Jackson 2007), the period which apparently also marked the evolution of melanism in cordylids (Daniels *et al*. 2004).

Although no truly melanistic form of any other lizard family besides the Cordylidae occurs in south-western South Africa, partly melanistic morphs of two burrowing skinks from the west coast have been described. Cordes & Mouton (1996) reported a melanistic morph of *Acontias meleagris* in the Saldanha-Langebaan area, that is in the same area where *C. niger* and a melanistic population of *C. polyzonus* occur. In this area, the dorsal half of the body of this burrowing skink is dark in colour, but not black as in the melanistic cordylids. Coastal populations of *Microacontias littoralis* contain melanistic as well as non-melanistic individuals of both sexes (Mashinini, Heideman & Mouton 2008). Again the dorsal half of the body may be darkly coloured. No information is available, but it is possible that individuals

position themselves in the surface layer of the sand with dorsal parts of the body partly exposed to the sun. On the other hand, the smooth, highly reflective skin surface of these skinks probably negates a significant role of colour in thermoregulation.

Several melanistic cordylid species/populations occur in association with a high incidence of cloud cover and fog. The role of melanism in improving heating rates under such conditions has been demonstrated (Clusella-Trullas *et al*. 2007a), but a significant role in protection against harmful UV radiation under the same conditions also remains a strong possibility. Partly cloudy and overcast conditions, and even summer haze, may sometimes result in increased levels of solar radiation (both UV and broadband) at ground level (Estupiñán *et al*. 1996; Long *et al*. 1996; McKenzie, Paulin & Kotkamp 1997; Sabburg & Wong 2000; Calbó *et al*. 2005; Adam & Shazly 2007). This is known as the cloud enhancement effect (Estupiñán *et al*. 1996), and enhancements of 20–30% above the expected cloudless radiation have been reported (Bordewijk *et al*. 1995). The co-occurrence of three melanistic lizard species and four melanistic molluscs at the Landdroskop locality (Mouton & Van Wyk 1990) casts some doubt on improved heating rates as the only explanation for melanism in cordylids, because molluscs are not heliothermic baskers and melanism should not play a significant role in thermoregulation.

In conclusion, several melanistic cordylid populations show a distinct association with a high incidence of fog and cloud cover, underscoring the thermal melanism hypothesis. Several other populations, however, do not show such an association. We conclude that the resolution of our analysis was not fine enough to capture localized high incidences of orographic fog and cloud cover at inland montane localities, resulting in an underestimation of climatic conditions experienced at many of the inland localities where melanistic cordylids occur. We also conclude that some melanistic species, such as *C. peersi* and *P. capensis* may

have a morphology providing them with great flexibility in habitat use, allowing them to overcome the constraints of melanism in warm environments.

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CHAPTER 3

MELANISTIC CORDYLIDS USE HIGH ROCKS IN WARM ENVIRONMENTS

3.1 INTRODUCTION

Melanism, that is, the occurrence of individuals that are darker in pigmentation, is common among reptiles and has been implicated in thermoregulation (e.g., Kettlewell 1973; Kingsolver & Wiernaz 1991; Clusella Trullas *et al*. 2007a), protection from ultraviolet radiation (Gunn 1998), cryptic coloration (e.g., Kettlewell 1973; Endler 1984), aposematism (e.g., Turner 1977), and sexual selection (e.g. Wiernasz 1989). Of these, its significance in thermoregulation has probably been best studied (see Clusella Trullas *et al*. 2007a for a review). The theory of thermal melanism proposes that under the same environmental conditions, melanistic individuals should heat faster and reach higher equilibrium temperatures than lighter coloured ones of similar body size (Gates 1980). Relative to lighter coloured individuals, melanistic individuals should therefore be at an advantage under conditions of low ambient temperature in that they can have extended periods of activity, increasing their overall evolutionary fitness. One of the key assumptions that underlie the thermal melanism hypothesis therefore is that melanistic diurnal species should inhabit cooler areas than lighter coloured species (Clusella Trullas *et al*. 2007a). Furthermore, should the limits of behavioural compensation be exceeded, melanistic species could be at a disadvantage in warm environments because overheating is likely to constrain activity (see Clusella Trullas *et al*. 2007a).

Six melanistic girdled lizard species occur in southern Africa (Mouton 1985, 1986a; Mouton and Oelofsen 1988; Mouton & Van Wyk 1995; Daniels, Mouton & Du Toit 2004). In line with the assumptions of the thermal melanism hypothesis, these species, with the

exception of one, have restricted distribution ranges in cool coastal or inland montane habitats (Mouton & Oelofsen 1988; Badenhorst 1990; Janse van Rensburg, Mouton & Van Niekerk 2009; Chapter 2) (Fig. 1). *Cordylus niger* and melanistic populations of *C. polyzonus*, for example, are restricted to localities along the west coast of South Africa where there is upwelling of cold water in the Atlantic Ocean and a high incidence of fog (Badenhorst 1990; Janse van Rensburg *et al*. 2009; Chapter 2). *Pseudocordylus nebulosus* and *C. oelofseni*, on the other hand, occur as isolated populations along the western section of the Cape Fold Mountains, seemingly in association with a high incidence cloud cover and orographic fog (Badenhorst 1990; Janse van Rensburg *et al*. 2009; Chapter 2).

Daniels *et al*. (2004) provided evidence that melanism in the *cordylus-niger-oelofseni* complex evolved during Miocene times, in other words, at the time of origin of the cold Benguela Current (Tankard & Rogers 1978; Siesser 1980; Hendey 1983). The present fragmented ranges of *C. niger* and *C. oelofseni* suggest that the climatic conditions with which melanism is associated today, sometime in the past occurred widely in south-western South Africa (Mouton & Oelofsen 1988; Daniels *et al*. 2004). After amelioration of climates, the ranges of melanistic forms fragmented, with populations surviving in cool refugia along the west coast and in the Cape Fold Mountains. Daniels *et al*. (2004) furthermore suggested that melanism in other cordylids also evolved during the same Miocene climatic event, in other words, that all melanistic cordylid populations are relics of melanistic species that thrived in south-western South Africa during an extended cool period during the Miocene.

In comparison to other melanistic cordylids, *P. capensis* and *C. peersi* have relatively extensive distribution ranges (Fig. 1), not giving the impression that they are relic forms. Although mostly occurring at mountain tops, *P. capensis* at places also occurs in warm lowland environments (Herselman, Mouton & Van Wyk 1992; Janse van Rensburg *et al*.

2009; Chapter 2). *Cordylus peersi* is seemingly restricted to a cooler enclave in Namaqualand, but the general area experiences warmer climates than those areas where the other melanistic species occur (Janse van Rensburg *et al*. 2009; Chapter 2). The distinct differences in range size among the six melanistic cordylid species (Fig. 1) suggest that these species may vary considerably in the degree to which melanism may act as a constraint in warmer environments. The wider distribution ranges of *P. capensis* and *C. peersi* relative to those of other melanistic cordylids, suggests that these two species may be better equipped for survival under warm conditions than the other melanistic cordylids.

In most lizard clades, preferred body temperature range is conservative at genus and family level and this is apparently also true for cordylids (Clusella Trullas *et al*. 2007b). It is therefore expected that, among melanistic cordylids, differences in the ability to survive in warmer environments will be related to differences in behaviour and habitat use rather than to differences in physiology. It has, for example, been shown that large rock formations provide a wider range of thermal habitats, including cooler ones, than smaller rocks (Huey *et al*. 1989; Adolph 1990; also see Chapter 4). Melanistic cordylids occupying large boulders or cliff faces should be able to overcome the constraints of melanism during warm weather conditions by making use of the cool microhabitats offered by this habitat type. Species will, however, differ in their ability to use large rocks, particularly in the ability to scale vertical surfaces (e.g., Wainwright & Reilly 1994). Biomechanical models, for example, have indicated that species occupying smooth vertical surfaces should have a flat body and head to keep the centre of mass close to the substrate (Vanhooydonck & Van Damme 1999; Zaaf *et al*. 1999, 2001; Zaaf & Van Damme 2001; Revell *et al*. 2007), and long limbs and distal segments to assist with jumping and running (Bels *et al*. 1992; Losos 1990; Van Damme, Aerts & Vanhooydonck 1998).

The aim of my study was to investigate differences in habitat use and morphology among melanistic cordylid lizards. I expected those melanistic cordylids of which the distribution ranges are extensive and include warmer environments, to prefer high rock formations that offer a wide range of microclimates, and to have long limbs allowing them to scale vertical rock surfaces.

3.2 Materials and Methods

3.2.1 Distributional data

Distributional data for the six melanistic cordylid taxa were obtained from CapeNature's State of Biodiversity database, which includes data from all major South African collections. *Cordylus niger* occurs as two isolated populations, one in the Saldanha-Langebaan area and one on the Cape Peninsula (Fig. 1). These two populations are genetically and morphologically indistinct (Mouton 1987; Brody *et al*. 1995; Daniels *et al*. 2004). Three melanistic populations of *C. polyzonus* occur along the west coast of South Africa, one in the Alexander Bay area, one in the Lambert's Bay area and one in the Saldanha-Langebaan area (Mouton & Oelofsen 1988; Badenhorst 1990) (Fig. 1). The taxonomic status of these populations is still uncertain. The Saldanha-Langebaan population, however, shows distinct morphological differences from the inland non-melanistic form (Mouton *et al*. 2002). *Cordylus oelofseni* occurs as three isolated populations along the western Cape Fold Mountains, one population in the Piketberg Mountains, one along the Olifantsrivier Mountains and one in the Hottentots Holland Mountains (Fig. 1). Mouton (1987) and Mouton & Van Wyk (1990) did not find any obvious morphological differences among the three populations, but Daniels *et al*. (2004) found genetic differences and suggested that the three populations may represent three distinct species. Formerly, *P. capensis* was partitioned into two subspecies, *P. c. robertsi* in

the north and *P. c. capensis* in the south (FitzSimons 1943). Herselman *et al*. (1992) found that, although different epiphenotypes predominate in the northern and southwestern parts of the distribution range, these epiphenotypes are connected by a continuum of variation. For the purposes of our study I partitioned *P. capensis* into a northern and a southern population, the dividing line following a natural break in the distribution (Fig. 1). *Cordylus peersi* and *P. nebulosus* occur as single populations in Namaqualand and in the Hottentots Holland Mountains, respectively (Fig. 1). I included 10 of the 12 populations described above in our analysis, leaving out the Alexander Bay and Lambert's Bay populations of *C. polyzonus*. The geographical limits of these two populations are not well-defined in the literature (Mouton *et al*. 2002).

3.2.2 Maximum temperature

Using GIS, the mean long term maximum temperature experienced at the recorded localities during the five hottest months (November–March), was calculated for each of the 10 melanistic cordylid populations. Because of their relatively extensive ranges, I further subdivided the two *P. capensis* populations by treating subpopulations recorded below 1000 m above sea level separately from those recorded above 1000 m.

3.2.3 Rock size preference

Rock size preference was determined for each of the 10 melanistic populations. At all selected localities where I obtained our data, the whole spectrum of rock sizes was available to lizards, from very small to very large. Only in the case of the two *P. capensis* populations, because of their extensive ranges, was it difficult to select representative localities for the survey of rock size preference. For the southern population, I selected the Landdroskop site in the Hottentots Holland Mountains, as *P. capensis* co-occurs with two

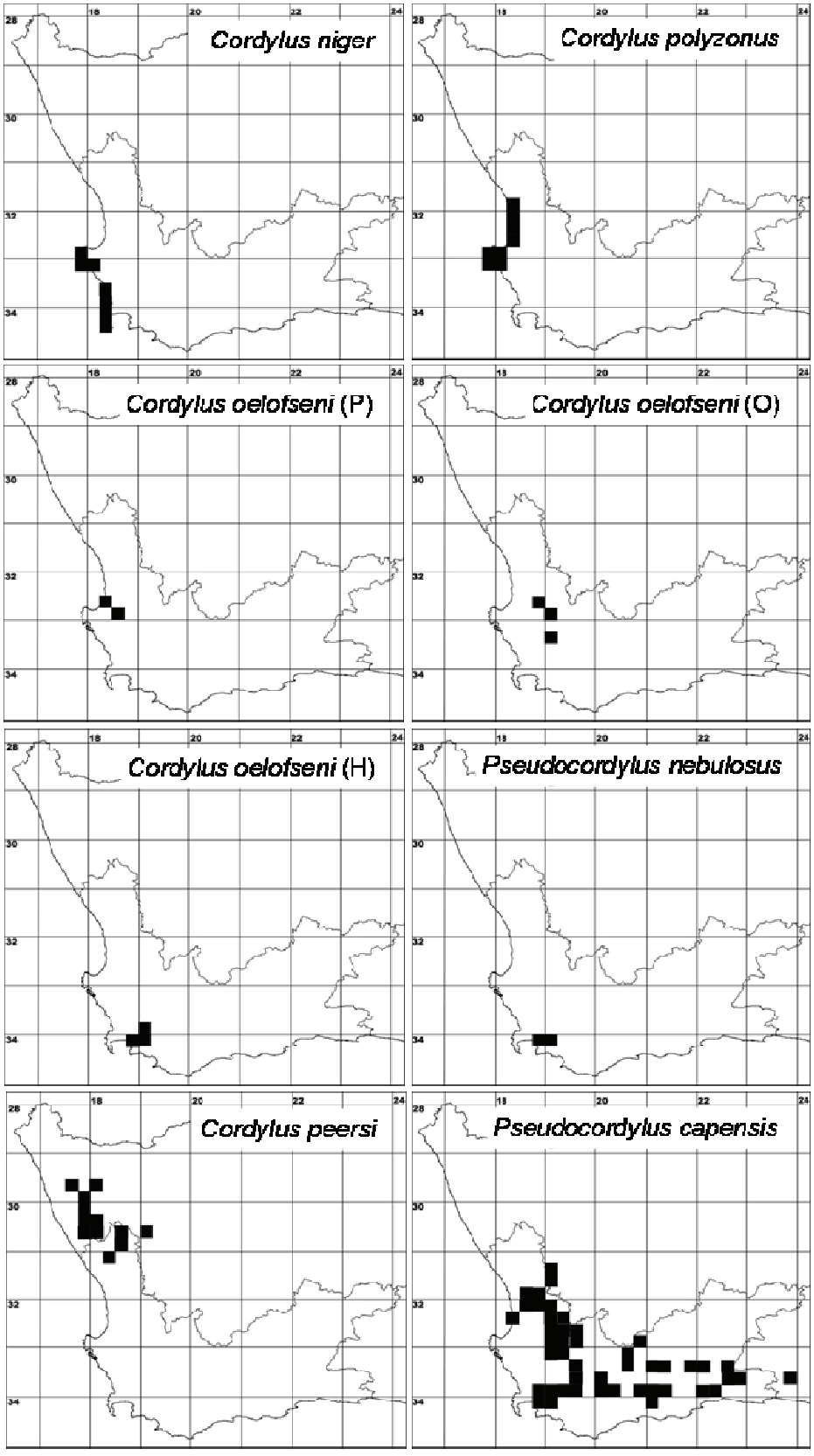

Figure 1. The distribution ranges (in quarter degree grid cells) of the eight melanistic cordylid species occurring in South Africa.

other melanistic species at this site, *C. oelofseni* and *P. nebulosus*, allowing direct comparison of the three species. For the northern population of *P. capensis*, I conducted the survey in the Matjiesrivier Nature Reserve in the Cederberg area. In addition, I recorded the habitat type at all the localities where *P. capensis* have been recorded to date. I classified the habitat type used by a population as mountainous terrain (high elevation, range of rock sizes readily available), boulder habitat (any elevation, mostly large rocks), cliff habitat (any elevation, large steep surfaces) or ravine habitat (any elevation, permanent/seasonal waterfall or stream present).

For each lizard observed in the field, the height of the rock on which the lizard perched (measured from ground level to the top of the rock), the perching height of the lizard, and the height of the crevice to which the lizard subsequently retreated (measured from ground level to the base of the crevice opening) were recorded. Rock height was categorized as being small (< 0.5 m high), medium (0.5-2.0 m high), and large (> 2.0 m high). For each species, the frequency of selection of rocks in each size class was calculated.

3.2.4 Morphology

Eight morphological measurements were recorded for preserved specimens of the 10 melanistic cordylid populations: snout-vent-length (SVL), tail length (TL), trunk length (TrL), longest toe of hind foot (LTHF), longest toe of front foot (LTFF), total hind limb length (Total HL), total front limb length (Total FL), and head height (HH). These variables were also recorded for *C. coeruleopunctatus*, a non-melanistic species belonging to the same clade as *P. capensis* and *P. nebulosus* (Frost *et al*. 2001). Morphological differences among these closely related species should indicate which characters may be adaptive for survival in environments where warm climate may be a constraint.

3.2.5 Statistical analyses

ANOVA, followed by Dunn's multiple pair wise comparisons, were used to compare selected rock heights, crevice heights and perch heights among species. Analysis of covariance (ANCOVA) with SVL as covariate was used to evaluate morphological differences among melanistic species. Lack of a corroborated phylogeny for the Cordylidae precluded the use of a comparative method in the analysis of our data.

3.3 RESULTS

3.3.1 Maximum temperature

Figure 2 shows that, of the melanistic cordylid populations investigated, the northern lowland subpopulations of *P. capensis* and the *C. peersi* population experience the highest mean annual maximum temperatures. The southern *C. oelofseni* population and the *P. nebulosus* population experience the lowest mean annual maximum temperatures for this period, more than 8°C lower than those recorded for the northern lowland *P. capensis* subpopulations and the *C. peersi* population. Of the 92 localities where *P. capensis* were found, 40 had a mean maximum temperature for November to March (the five hottest months) of 26°C or higher. Of these 62% were found in the northern part of the species distribution range.

3.3.2 Rock height preference

Significant differences in selected rock height, crevice height and perching height among the populations were recorded (rock height: $F = 117.49$, df = 9.00, $P < 0.001$; crevice height: $F = 70.53$, df = 9.00, $P < 0.001$; and perching height: $F = 43.89$, df = 8.00, $P < 0.001$). Mean values recorded for the 10 melanistic populations are listed in Table 1. Individuals of the northern population of *P. capensis* frequented significantly higher rocks

than individuals of all other melanistic populations (Table 2a). The majority of *P. capensis* individuals from the northern population were observed on large rock formations of 10 m or higher. Mean values recorded for the southern *P. capensis* population and for *C. peersi* were significantly higher than those for the two *C. niger* populations, the *C. polyzonus* population and the southern *C. oelofseni* population, but did not differ significantly from the values recorded for *P. nebulosus* and the two northern populations of *C. oelofseni* (Table 2a). The mean value recorded for *C. oelofseni* in the Olifantsrivier Mountains (north) was also significantly higher than that recorded for *C. oelofseni* in the south.

The majority of *C. niger* and *C. polyzonus* individuals were found on small and medium sized rocks, with less than 4 % of the lizards selecting rocks higher than 2.0 m (Table 3). Individuals of *P. nebulosus* and the three *C. oelofseni* populations selected rocks in all size classes although the majority of individuals occurred on medium sized rocks (Fig. 3, Table 3). *Cordylus peersi* also selected medium sized rocks, although a large percentage (nearly 40%) of individuals were found on large rocks (Fig. 4). In comparison to other melanistic cordylids, the majority of *P. capensis* individuals were found on large rocks (Fig. 5 & 6, Table 3). While only a small percentage of *C. peersi* individuals were found on small rocks, *P. capensis* individuals were never found in this microhabitat. In fact, individuals of the northern population of *P. capensis* were exclusively associated with rocks > 2.0 m in height.

Individuals in the northern population of *P. capensis* selected crevices that were significantly higher than those selected by individuals of other melanistic populations (Table 2b). Individuals of *C. peersi* and the southern population of *P. capensis* selected crevices that were significantly higher than those selected by individuals of the two *C. niger* populations, the *C. polyzonus* population and the southern *C. oelofseni* population, but not significantly higher than those recorded for *P. nebulosus* and the two northern

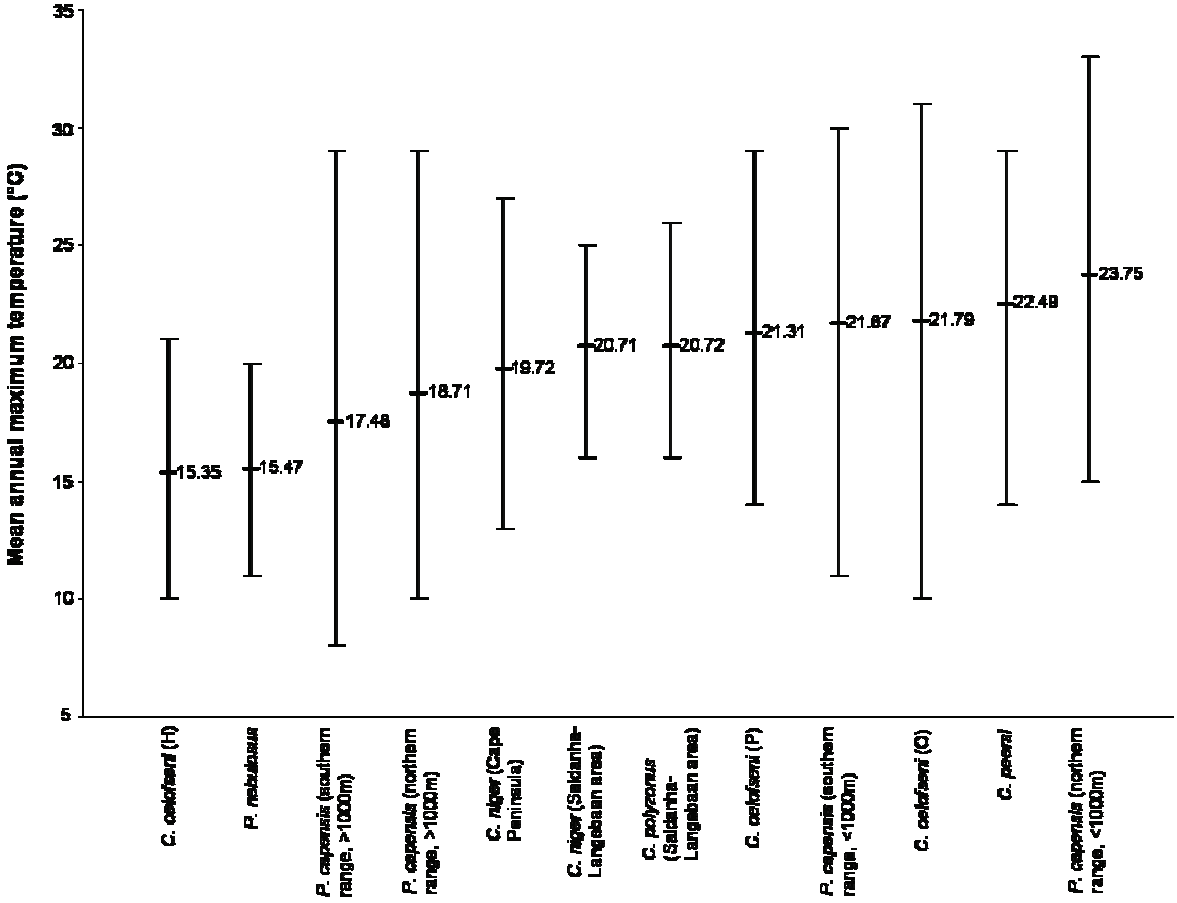

Figure 2. Mean annual maximum temperatures at the localities where melanistic cordylid species occur. Mean minimum and maximum are indicated by the vertical bars.

Table 1. Summary of distribution range size and mean habitat use and morphological variables for eight melanistic cordylids (the three *C. oelofseni* populations were considered as distinct species). Means ± SE are shown.

Species	***P. capensis* (north)**	***P. capensis* (south)**	***P. nebulosus***	***C. peersi***	***C. polyzonus***	***C. oelofseni* (H)**	***C. oelofseni* (O)**	***C. oelofseni* (P)**	***C. niger* (north)**	***C. niger* (south)**
Distribution range (km^2)	36558.87		14.97	1545.12	2183.79	80.39	1020.08	73.47	-	410.73
Habitat use										
N	34	50	48	66	50	60	50	16	54	25
Rock height ± SE (cm)	825.00 ± 61.77	230.82 ± 16.49	154.35 ± 18.97	196.64 ± 11.73	75.10 ± 7.08	54.33 ± 3.66	165.20 ± 9.88	103.13 ± 13.16	81.37 ± 7.49	73.60 ± 8.96
Crevice height ± SE (cm)	421.78 ± 40.46	126.27 ± 13.84	70.71 ± 11.72	131.03 ± 9.50	18.70 ± 5.89	16.27 ± 2.87	92.24 ± 6.95	40.63 ± 6.86	30.22 ± 5.49	33.60 ± 7.50
N	29	45	43	No data	36	40	21	13	26	24
Perching height ± SE (cm)	459.66 ± 49.92	180.82 ± 14.31	99.56 ± 12.72	No data	74.44 ± 8.55	46.88 ± 4.78	90.29 ± 9.57	61.92 ± 8.39	89.50 ± 10.71	61.79 ± 7.88
Morphology										
N	11	17	7	10	19	12	20	10	17	10
SVL (mm)	96.47 ± 1.76	89.52 ± 2.64	71.76 ± 1.28	76.49 ± 1.73	99.02 ± 2.29	60.30 ± 0.88	60.67 ± 0.79	59.82 ± 1.12	77.88 ± 1.67	73.42 ± 2.30
Tail length (mm)	140.57 ± 3.75	130.30 ± 3.85	94.24 ± 3.18	82.90 ± 2.73	114.31 ± 3.08	67.75 ± 7.89	60.77 ± 4.46	60.03 ± 5.67	78.91 ± 3.28	80.58 ± 3.68
Trunk length (mm)	38.51 ± 1.94	34.45 ± 1.36	26.62 ± 1.85	30.85 ± 1.14	39.85 ± 1.24	25.25 ± 0.70	25.44 ± 0.55	24.76 ± 0.83	31.39 ± 1.05	30.14 ± 1.26
4th toe (mm)	15.21 ± 0.28	14.03 ± 0.28	10.88 ± 0.47	9.98 ± 0.19	11.27 ± 0.24	8.26 ± 0.20	7.84 ± 0.12	7.74 ± 0.11	10.48 ± 0.33	10.49 ± 0.32
4th finger (mm)	11.73 ± 0.35	9.49 ± 0.48	7.62 ± 0.24	7.44 ± 0.21	8.79 ± 0.18	6.21 ± 0.14	5.79 ± 0.10	5.66 ± 0.08	7.56 ± 0.27	7.45 ± 0.18
Total hind limb (mm)	63.25 ± 0.75	55.76 ± 1.11	40.05 ± 1.44	43.95 ± 0.47	55.66 ± 1.20	33.53 ± 0.48	33.53 ± 0.41	33.22 ± 0.42	41.14 ± 1.06	39.82 ± 1.15
Total front limb (mm)	45.95 ± 0.53	38.06 ± 1.19	28.63 ± 0.79	31.47 ± 0.50	40.58 ± 0.96	24.40 ± 0.30	23.75 ± 0.33	23.26 ± 0.35	29.49 ± 0.74	27.83 ± 0.72
Head height (mm)	11.61 ± 0.68	11.46 ± 0.45	8.40 ± 0.20	8.97 ± 0.23	11.69 ± 0.31	7.23 ± 0.12	6.90 ± 0.12	6.73 ± 0.78	10.07 ± 0.35	9.54 ± 0.33

Table 2. Summary of the post hoc comparison (Sheffé) showing significant differences in (a) rock height and (b) crevice height selected by individuals of 10 melanistic cordylid populations. Significant differences are indicated in bold.

(a)	**Species**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
1	*C. niger* (north)										
2	*C. niger* (south)	1.000									
3	*C. oelofseni* (H)	0.998	0.999								
4	*C. oelofseni* (P)	0.999	0.999	0.993							
5	*C. oelofseni* (O)	0.245	0.454	**0.013**	0.966						
6	*C. peersi*	**0.004**	**0.046**	**0.000**	0.625	0.994					
7	*C. polyzonus*	1.000	1.000	0.999	0.999	0.175	**0.002**				
8	*P. capensis* (north)	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**			
9	*P. capensis* (south)	**0.000**	**0.002**	**0.000**	0.191	0.657	0.990	0.000	**0.000**		
10	*P. nebulosus*	0.481	0.660	0.054	0.991	1.000	0.958	0.376	**0.000**	0.435	

(b)	**Species**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
1	*C. niger* (north)										
2	*C. niger* (south)	1.000									
3	*C. oelofseni* (H)	0.999	0.999								
4	*C. oelofseni* (P)	1.000	1.000	0.999							
5	*C. oelofseni* (O)	0.159	0.579	**0.015**	0.892						
6	*C. peersi*	**0.000**	**0.008**	**0.000**	0.130	0.774					
7	*C. polyzonus*	0.999	0.999	1.000	0.999	**0.040**	**0.000**				
8	*P. capensis* (north)	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**			
9	*P. capensis* (south)	**0.000**	**0.030**	0.000	0.236	0.924	1.000	**0.000**	**0.000**		
10	*P. nebulosus*	0.788	**0.964**	0.320	0.998	0.998	0.151	0.463	**0.000**	0.363	

Table 3. Percentage individuals in each melanistic cordylid population observed on small, medium and large rocks, respectively.

Species	***N***	**S (<0.5 m)**	**M (0.5 – 2.0 m)**	**L (>2.0 m)**
P. capensis (north)	34	0.00	0.00	100.00
P. capensis (south)	50	0.00	46.00	54.00
P. nebulosus	48	10.42	68.75	20.83
C. peersi	66	3.03	59.09	37.88
C. polyzonus	50	40.00	58.00	2.00
C. oelofseni (H)	60	46.67	53.33	0.00
C. oelofseni (O)	50	6.00	70.00	24.00
C. oelofseni (P)	16	6.25	87.50	6.25
C. niger (north)	54	35.19	61.11	3.70
C. niger (south)	25	32.00	68.00	0.00

Figure 3. Typical habitat of *Cordylus oelofseni* (a), and a typical small rock (< 50 cm) (b).

Figure 4. Typical habitat of *Cordylus peersi* in Namaqualand.

Figure 5. Typical mountainous habitat of *Pseudocordylus capensis* in the southern parts of its distribution.

Figure 6. Typical habitat of *Pseudocordylus capensis* in the northern parts of the species' distribution range: (a) boulders, (b) cliff faces, and (c) ravine.

populations of *C. oelofseni* (Table 2b). *Cordylus oelofseni* (O) selected significantly higher crevices than *C. oelofseni* (H) (Table 2b). *Pseudocordylus capensis* (northern population) perched significantly higher than all the other melanistic populations ($P < 0.001$ for all cases), including the southern population of *P. capensis* ($P < 0.001$). There was no significant difference in perching height among the rest of the melanistic species, except for *P. capensis* (southern population) that perched significantly higher than *C. niger* (southern population) ($P < 0.05$) and *C. oelofseni* (H) ($P < 0.001$).

Of the 40 *Pseudocordylus capensis* populations which experienced a mean maximum temperature of 26°C or higher during November to March, 25 occurred in northern parts and 15 in the southern parts of the species' distribution range. Of the southern populations, 40% were exclusively associated with mountainous terrain, while the other populations were found in a combination of boulder, cliff and waterfall habitats. In the north, 100% of the populations were associated with large boulders, high vertical cliffs, waterfalls or ravines, or a combination of these habitats, even those populations occurring in mountainous terrain (Fig. 6).

3.3.3 Morphology

The species displayed significant differences in terms of morphology (ANCOVA: $F = 163.05$, $P = 0.001$). Average values for morphological variables are summarized in Table 1. The northern and southern populations of *Pseudocordylus capensis* did not differ in tail length ($P = 0.25$), but individuals from the northern population had a significantly longer tail than all other melanistic cordylids ($P < 0.001$ for all cases). Individuals from the southern population also had longer tails than other species ($P < 0.01$ for all cases), but did not differ from *P. nebulosus* ($P = 0.133$) and *C. polyzonus* ($P = 0.941$). *Pseudocordylus nebulosus* only had a significantly longer tail than *C. oelofseni* (H) ($P > 0.001$). *Cordylus*

polyzonus also had a significantly longer tail than *C. niger* (northern and southern populations) and the three *C. oelofseni* populations. The southern *Cordylus oelofseni* population had the shortest tail of all melanistic populations.

Species displayed considerable variation in trunk length. *Cordylus polyzonus* had the longest trunk of all melanistic cordylid species ($P < 0.001$ for all cases), and only did not differ from *P. capensis* (northern population, $P = 0.97$). *Pseudocordylus capensis* (northern population) differed from all other species ($P < 0.01$ for all cases), while *P. capensis* (southern population) only did not differ from *C. niger* (northern populations) ($P = 0.05$). *Cordylus oelofseni* (P) had the shortest trunk, and only did not differ from *P. nebulosus* ($P = 0.96$) and *C. oelofseni* (O) ($P = 0.99$).

There was very little variation in the length of the fourth toe among the 10 populations, the only significant difference being that the southern population of *P. capensis* had a longer fourth toe than *C. oelofseni* (O) ($P < 0.05$). Both northern and southern populations of *P. capensis*, however, had a significantly longer fourth finger (front limb) than all other populations ($P < 0.05$ for all cases), with the southern population only not differing from *C. polyzonus* ($P = 0.79$). *Cordylus peersi* had a significantly longer fourth finger than *C. oelofseni* (O) ($P < 0.05$) and *C. oelofseni* (P) ($P < 0.05$).

The northern and southern populations of *P. capensis* had the longest front and hind limbs of all melanistic cordylid species ($P < 0.01$ for all cases). The two populations did not differ significantly from each other ($P = 0.99$) or from *C. polyzonus* ($P = 0.18$ and $P = 0.35$, respectively) in terms of hind limb length, but the northern population of *P. capensis* did differ significantly from all populations in terms of front limb length ($P < 0.001$ for all cases). *Cordylus polyzonus* had significantly longer front limbs than all other species ($P < 0.001$ for all cases), and significantly longer hind limbs than the species in the *oelofseni*-complex, *C. niger* and *P. nebulosus* ($P < 0.05$ for all cases). *Cordylus peersi* and *C. niger*

(northern and southern populations) had significantly longer front limbs than the members of the *oelofseni*-complex ($P < 0.01$ for all cases), while *C. peersi* also had significantly longer front limbs than the southern population of *C. niger* ($P < 0.05$). *Pseudocordylus nebulosus* did not differ in front limb length from *C. peersi* ($P = 0.26$) and the two *C. niger* populations ($P = 0.99$ for both cases). The members of the *oelofseni*-complex had the shortest front limbs of all melanistic cordylids.

Pseudocordylus capensis (northern and southern populations) and *C. polyzonus* had higher heads than all other melanistic species ($P < 0.001$ for all cases). *Cordylus peersi* and *C. niger* had higher heads than the members of the *oelofseni*-complex ($P < 0.001$ for all cases).

There were significant morphological differences among the members of the *coeruleopunctatus-nebulosus-capensis*-clade ($F = 46.59$, $P < 0.001$). Toe length (hind foot) was the only variable that did not differ significantly between the four populations ($P > 0.05$). The northern *P. capensis* population had a significantly longer tail, trunk and front limbs than the southern population ($P < 0.05$ for all cases). However, both *P. capensis* populations had significantly longer total limb and tail lengths than the other two species ($P < 0.05$ for all cases). There were no significant morphological differences between *P. nebulosus* and *C. coeruleopunctatus*.

3.4 DISCUSSION

The close relationship between habitat use and morphology has been well-documented for several lizard groups (Herrel, Meyers & Vanhooydonck 2001; Kohlsdorf, Garland & Navas 2001; Schulte *et al*. 2004; Elstrott & Irschick 2004; Goodman 2005; Irschick *et al*. 2005a, 2005b) and is also apparent in the melanistic cordylid species of southern Africa. In this study, I found that those melanistic species not restricted in their distribution to cool

coastal or montane localities, prefer large boulders and cliff faces as habitat. With the exception of *Cordylus oelofseni*, these species also have relatively long limbs, which probably assist in scaling vertical surfaces. The species with the longest legs, *Pseudocordylus capensis*, also has the most extensive distribution range of the six melanistic cordylid taxa.

Although, throughout its range, *P. capensis* mostly occurs along mountain tops, it does at many places also occur in warm lowland environments. My data show that at these lowland localities, this species is invariably associated with a very distinct habitat type, either waterfalls, ravines, huge piled up rock formations or huge boulders. Huey *et al*. (1989) investigated retreat-site selection by garter snakes during summer, and demonstrated that there is a difference in the thermal properties of large and small rocks. These snakes almost always avoided small rocks, as these reached higher maximum temperatures than larger rocks, which would result in the snake selecting such a rock to die of heat stress in the mid-afternoon (also see Chapter 4). Adolph (1990) reported that lizards occurring at lower, warmer elevations chose higher perches than lizards found at higher, cooler elevations. This author also reported a 2–5°C decrease in operative temperatures from perches near the ground (0–0.25 m) to perches higher than 1 m. The operative temperature experienced by a lizard in a certain microclimate may thus be influenced by perch height, as lower perches experience higher operative temperatures than higher perches because of an increase in ambient temperature and a decrease in wind speed near ground level (Geiger 1965; Stevenson 1985).

The almost exclusive association of *P. capensis* populations in the warmer northern part of its range with high rock formations and vertical cliff faces suggests that this habitat type may be crucial for the survival of a melanistic cordylid in a warm environment (Chapter 4). At the same time, *P. capensis* illustrates that the possible constraints of

melanism in warm environments can be overcome by a more flexible use of the habitat and that melanistic reptiles do not have to be restricted to cool environments, as is assumed by the thermal melanism hypothesis (Clusella Trullas *et al*. 2007a).

To effectively use the wide range of microclimates offered by high rock formations in thermoregulation (Chapter 4), the lizards must be able to scale vertical surfaces with comfort. For this, a specialized morphology may be required. In my study, the two species using the highest rock formations have long legs and I assume that long legs are a requirement for living on large boulders and cliffs. Losos *et al*. (2002) investigated escape behaviour in cordylids and scored the species according to use of vertical substrates. *Pseudocordylus capensis* and *C. peersi* (both species having relatively long limbs and occupying large rock formations), were given high scores for the use of vertical surfaces.

Of the six melanistic cordylid taxa, the two sister species, *P. capensis* and *P. nebulosus* (Frost *et al*. 2001) have the most extensive and the most restricted ranges, respectively. In morphology, *P. nebulosus* is very similar to *C. coeruleopunctatus*, the basal species in the clade (Frost *et al*. 2001), suggesting that the long limbs of *P. capensis* is a derived character. Daniels *et al*. (2004) suggest that melanism in the different cordylid clades evolved sometime during the Miocene in response to the development of the Cold Benguela current and general cooling down of climates along the south-western coastal regions of South Africa. The preliminary results of a molecular analysis indicate that the northern *P. capensis* populations may be basal in the species (M.J. Cunningham, pers. comm.). It is therefore a strong possibility that an ancestral melanistic species, very similar to *P. nebulosus* in morphology, during a cool period had an extensive range reaching as far north as the Gifberg area (northernmost population). During subsequent amelioration of climates, the ancestral melanistic population fragmented into northern and southern subpopulations. With the lack of suitable cool refugia in the northern Cape Fold

Mountains, further amelioration of climates resulted in the evolution of longer limbs and a streamlined body enabling this form to use the physical environment more effectively in thermoregulation. After the evolution of this adaptation, the species would have expanded its range to the present extensive one.

Although the three *C. oelofseni* populations do not show any significant morphological differences, they do differ in habitat use. The GIS analysis revealed that the northern, Olifantsrivier Mountains population is associated with a much warmer climate than the southern, Hottentots Holland Mountains population (Fig. 2). It is noteworthy that the northern population utilizes significantly higher rock formations than the southern population, again highlighting the possibility that the use of high rock formations may be essential for the survival of melanistic cordylids in warm environments.

In conclusion, the results obtained in my study suggest that those melanistic cordylids that are presently not restricted to cool environments are able to survive in warm environments by using large rock formations with their associated wider range of thermal opportunities (Chapter 4). The use of these habitats, however, requires a specific morphology, notably longer limbs. The results of my study furthermore show that melanistic reptiles do not have to be restricted to cool environments, as assumed by the thermal melanism hypothesis, and that the possible constraints of melanism in warm environments can be overcome by more flexible use of the habitat.

CHAPTER 4

MELANISTIC CORDYLIDS IN WARM ENVIRONMENTS: THE ROLE OF HABITAT USE IN FACILITATING INCREASED THERMAL QUALITY AND ACTIVITY TIME IN *PSEUDOCORDYLUS CAPENSIS*

4.1 INTRODUCTION

Temperature regulation plays an integral part in lizard ecology and behaviour (Huey 1982). Lizards can reduce the influence of changes in the thermal environment by genetic differentiation among populations, physiological mechanisms, and behavioural shifts (Slobodkin & Rapoport 1974; Dzialowski & O'Connor 1999). The latter is believed to be the primary compensatory mechanism in most lizards (Bogert 1949; Huey & Slatkin 1976; Kearney, Shine & Porter 2009), and may include shifts in habitat selection, shuttling, restriction of activity times, and postural adjustments to alter heat exchange rates (i.e. Heath 1965; Hammel, Caldwell, & Abrams 1967; Spellerberg 1972; Huey, Pianka & Hoffman 1977; Hertz & Huey 1981; Van Damme *et al*. 1989; Castilla & Bauwens 1991).

The thermal melanism hypothesis predicts that a dark coloured lizard will heat up faster than a light coloured one under the same environmental conditions (Norris 1967; Kettlewell 1973; Gates 1980; Clusella Trullas, Van Wyk & Spotila 2009). Melanism has thus often been considered an adaptation to cool environments where increased heating rates would be an advantage (Cole 1943; Carlquist 1965; Norris 1967; Hoppe 1979; see Clusella Trullas, Van Wyk & Spotila 2007a for a review). Clusella Trullas *et al*. (2009) compared pairs of melanistic and non-melanistic models of three cordylid species under the same microclimatic conditions. In summer, the habitat mean thermal quality (d_e,

defined as the deviation between operative (T_e) and preferred body (T_{pref}) temperatures (Hertz, Huey & Stevenson 1993)) of melanistic lizards was lower than that of non-melanistic lizards ($d_{e\ mel} > d_{e\ non\text{-}mel}$). The operative temperatures (T_es) of non-melanistic models were below the T_{pref}s for a longer period of time than the T_es of melanistic models. On a cold day, however, the habitat mean thermal quality for the melanistic cordylid lizards was better than for non-melanistic ones, i.e. there was a greater overlap of T_e and T_{pref} ($d_{e\ mel} < d_{e\ non\text{-}mel}$). Where increased heating rates in cool environments may thus result in increased activity times of melanistic lizards (see Clusella Trullas *et al*. 2007a for a review), increased equilibrium temperatures in warm environments may necessitate decreased activity times of melanistic lizards to avoid overheating ($T_e > T_{pref}$). However, Clusella Trullas *et al*. (2007a) suggested that differences in physiology and/or behaviour between species may confound the effects of melanism. This view is corroborated by a similar suggestion for *Liolaemus* lizards (Rodríguez-Serrano, Navas & Bozinovic 2009). The authors suggested that behavioural thermoregulation and/or an evolutionary flexible physiology resulted in these lizards inhabiting habitats ranging from lowlands to montane environments.

The melanistic cordylid species occurring in southern Africa (Mouton 1985, 1986a; Mouton & Oelofsen 1988; Mouton & Van Wyk 1995; Daniels, Mouton & Du Toit 2004) vary considerably in morphology, habitat selection and distribution (Chapter 3). Most species have short limbs, are associated with small rocks (< 50 cm in height), and have restricted distributions in coastal and montane localities. In contrast, the Graceful Crag Lizard, *Pseudocordylus capensis*, has relatively long limbs and a wide distribution (Chapter 3). It is mainly associated with large boulder and cliff habitats, and is found at both highland and lowland localities (FitzSimons 1943; Mouton 1985; Herselman, Mouton & Van Wyk 1992; Bauer & Branch 1995; Janse van Rensburg, Mouton & Van Niekerk

2009; Chapter 2; Chapter 3). Specifically the northern populations of *P. capensis* are mainly associated with warmer environments (Janse van Rensburg *et al*. 2009; Chapter 2).

It has been suggested that the slender body and relative long limbs of *P. capensis* allow for the successful utilization of large rock formations (Chapter 3). The increase in air temperature and decrease in wind speed near ground level (Geiger 1965; Stevenson 1985), result in lower perches (0 - 0.25m above ground) having higher T_es than higher perches (> 1m above ground) (Adolph 1990). Due to differences in size and physical structure, large and small rock formations also differ in their availability of thermally suitable microhabitats. Large rock formations often have large shaded areas thus offering more temperate microhabitats, whereas small rocks receive more solar radiation and may reach much higher temperatures than large rock formations (Huey *et al*. 1989). Utilization of larger rock formations should provide *P. capensis* with a wider range of T_es, or in the definition of the niche concept, extend the multidimensional climatic space (niche) (Kearney & Porter 2004) of this species.

Due to the wider range of available T_es, a lizard on a large rock will be exposed to more extreme temperatures, implicating a lower mean T_e but with higher variability. The lower the mean T_e the lower the mean d_e value will be, and thus a better match. According to the cost-benefit scenario, the thermal quality of a specific environment is directly associated with the costs (time and energy) of thermoregulation to match T_b with T_{pref} (Row & Blouin-Demers 2006). On the one hand, Huey & Slatkin (1976) suggested that in extreme warm environments, lizards may abandon thermoregulation because of the costs and rather conform, whereas on the other hand, Blouin-Demers & Weatherhead (2001) suggested that conformation in extreme cold environments will compromise fitness since low T_b will translate to poor performance. It may therefore be argued that ectotherms will

thermoregulate more effectively when the thermal quality is low (Blouin-Demers & Weatherhead 2001; Row & Blouin-Demers 2006).

According to Kearney *et al*. (2009), the ability of an ectotherm to buffer increases in air temperature by behavioural means is dependent on the availability of shade (or other cool environments). The availability of thermally suitable microhabitats and the ability of a lizard to utilize its habitat will thus be crucial factors determining whether a melanistic cordylid will be able to survive in a warm environment. Thus, in addition to the morphological differences associated with differences in habitat selection between *P. capensis* and the other melanistic cordylid species (Chapter 3), I expect *P. capensis* to also display behavioural differences (i.e. in habitat use and activity) as an adjustment/adaptation to the habitat it occurs in.

In this study, I aimed to answer three basic questions: 1) On a hot summer day, do melanistic lizards occurring on large rock formations differ in their daily activity patterns from melanistic lizards occurring on small rock formations?; 2) How does thermal quality (for *P. capensis*) vary between large and small rock formations?; and 3) Does *P. capensis* display shifts in habitat use across seasons?

By shuttling between the range of microhabitats provided by large rock formations, and selecting suitable microhabitats, I expect *P. capensis* to increase its activity time, thus allowing this species to survive in warm environments. I predict *P. capensis* to have a longer activity period than a melanistic cordylid species that has short limbs and occurs on small rocks. It is expected that a large rock formation will provide a better thermal quality habitat (good match between T_e and T_{pref}) for *P. capensis* than a small rock (mismatch between T_e and T_{pref}). Lizards also often display shifts in habitat use across seasons (Christian, Tracy & Porter 1983; Webb & Shine 1998; Bishop & Echternacht 2004). In the northern parts of its distribution range, *P. capensis* is associated with large boulders,

vertical cliff faces or ravines (Chapter 3). In summer, a ravine may provide a sufficient number of cool microhabitats for *P. capensis* to survive in warm environments, but during the cooler seasons, the ravine may be too cold for lizards to be active due to increased shade area (pers. obs.). During cooler seasons, it may thus be necessary for *P. capensis* individuals to move to warmer (more direct solar radiation) microhabitats. I therefore also investigated whether *P. capensis* occurring in a ravine situation display any habitat shifts across seasons.

4.2 MATERIALS AND METHODS

4.2.1 Study areas and species

Data on daily activity patterns and operative temperatures (T_e) available to *Pseudocordylus capensis* on small and large rock formations were collected on hot sunny days at Landdroskop in the Hottentots Holland Mountains, Western Cape, South Africa (34°2'57" S, 18°59'30" E; altitude 1000 m a.s.l.). This site was selected because the distribution of *P. capensis*, a melanistic species with long limbs mainly found on rocks > 2 m in height, and *Cordylus oelofseni*, a melanistic species with short limbs mainly found on rocks < 2 m in height, overlaps in this area. This provided the opportunity to compare the daily activity patterns of two melanistic species with different morphologies and habitat selections under the same environmental conditions. It also allowed for the simultaneous calculation of habitat thermal quality index (d_e, Hertz *et al*. 1993) for *P. capensis* on large and small rock formations in an area where both types are occupied by melanistic cordylid species.

I investigated whether *P. capensis* displays shifts in habitat use across seasons in the northern part of the species distribution range where populations are associated with relatively warm climatic conditions (Janse van Rensburg *et al*. 2009; Chapter 2). Observations were conducted at Gifberg Holiday Farm in the Gifberg Mountains

(31°48'34" S, 18°47'35" E). Populations in this area are found in ravines with seasonal waterfalls.

4.2.2 Daily activity patterns

Data on the daily activity patterns of *P. capensis* and *C. oelofseni* were collected on two consecutive days during March 2006 (late summer), and again for a day during January 2007 (mid-summer). Two transects of 150 m each were laid out, one for each species in an area where the concentration of a particular species was high. Two observers (one per transect) walked along each transect once every hour between 0800 and 1800, taking 20-40 minutes to complete the distance. For each time slot, the number of active lizards was recorded, and the highest number recorded was regarded as the population size. From this the percentage of each population active during each time slot was calculated. Data on rock height, perch height and sun exposure were recorded for each active lizard. General climatic data for the specific days were obtained from the weather station at Landdroskop monitored by the local conservation agency, CapeNature. Hourly activities (as a percentage of the total population) of the two populations were compared by means of *Z*-tests.

4.2.3 Operative environmental temperatures

Pseudocordylus capensis specific operative temperatures (T_e) were collected at Landdroskop during March 2008 (late summer). Operative temperatures were determined by means of cylindrical copper models. These models represented *P. capensis* in size and were painted with a colour (Desert Darkness, Dulux, reflectance 11.33%) that resembled the lizard's average dorsal reflectance in the 200-1100 nm spectral range (visible and near infrared spectrum). Reflectance was measured on the dorsal area by means of an Ocean

Optics USB 2000 spectrophotometer and a PX-2 xenon lamp (Florida, USA). Reflection was recorded using a probe held normal to the surface, collecting light from a spot of 6 mm in diameter. A white reference (Spectralon 99% white standard) and a dark reference were taken for calibration. A DS1921G-F5 Thermochron iButton was fitted inside each model and held in place with a piece of re-usable adhesive (Prestik, Bostik Co., South Africa). Models were sealed at the ends with cork and silicon glue.

Models were calibrated by testing a model and a live lizard side by side to determine the similarity of temperature responses. A model and a live lizard were placed on a cardboard surface; the lizard was restrained by ties around the shoulders, pelvis and base of the tail. A heat lamp (100 W, Osram, Germany) was suspended one meter above the model and lizard. The lizard and model equilibrated to room temperature (± 20°C) before the trail started. The light was switched on, and after the lizard and model equilibrated to the new conditions (i.e. body temperature did not change more than 0.1° in 5 min.), the light was lower by 5 cm. This was repeated until the light was suspended about 40 cm above the lizard and the model. The relationship of lizard body temperature (T_b) against T_e was very close to linear (one) ($y = 0.7985x + 8.4865$, $R^2 = 0.9763$). The accuracy of the thermometer was 1°C, and the mean difference in absolute value between the model and lizard was less than 1°C, and I can therefore assume that the model provides me with T_es close to the T_b of *P. capensis*.

In the field, the T_e-models were placed on six large rocks measuring at least 2 m in height, and six small rocks measuring no more than 50 cm in height. Each small rock had two T_e-models – one north-facing and one south-facing (two microsites, n = 12). Each large rock had six T_e-models, three facing north and three facing south (six microsites, n = 36). On each face one T_e-model was placed near the bottom of the rock (below 50 cm), one at a height of at least 2 m above ground, and a third halfway in between the top and bottom

models. T_e-models recorded data for a period of 10 days (including hot and rainy days). Only T_es recorded between 0900 and 1800 were used in calculations.

4.2.4 Preferred body and set-point temperatures

Preferred body temperature (T_{pref}) of *P. capensis* was determined in a thermal gradient setup in the laboratory (Fig. 1). Six adult lizards were individually placed in a terrarium measuring 130 x 30 x 30 cm. The floor of each terrarium was covered with gravel. Lizards were visually isolated from each other, and a gauze sheet was placed over the terrariums to prevent lizards from escaping. Ambient temperature was kept constant at 20°C ± 1°C. A 250 W infrared lamp suspended 50 cm above the one end of each terrarium provided the lizard with a thermal gradient ranging from 50°C to 20°C. Lizards were subjected to a 12:12 hour dark light cycle. Each terrarium had a shelter made from ceramic tiles and wooden spacers running the length of the terrarium. This excluded the possibility that a lizard will act “unnaturally” because it feels unsafe in the presence of no shelter, or that the lizard will favour a specific temperature due to only one shelter provided at one end of the terrarium. Lizards were not fed one day before and during the trail, but water was available *ad libitum*.

A Type K thermocouple was inserted into the cloaca of each individual and fixed to the lizard at the base of the tail with a piece of surgical tape (Elastoplast, Beiersdorf AG, South Africa). The thermocouple was then threaded through the centre of the gauze, suspending it above the terrarium floor and allowing for free movement of the lizard. The thermocouples were all connected to a USB TC-08 Temperature Logger (Pico Technology Ltd.) that recorded body temperature (T_b) once every minute. This allowed for data to be recorded on a continuous basis for three consecutive days without disturbing the lizards. An observer did however check in on the lizards each morning at 0800 and again after

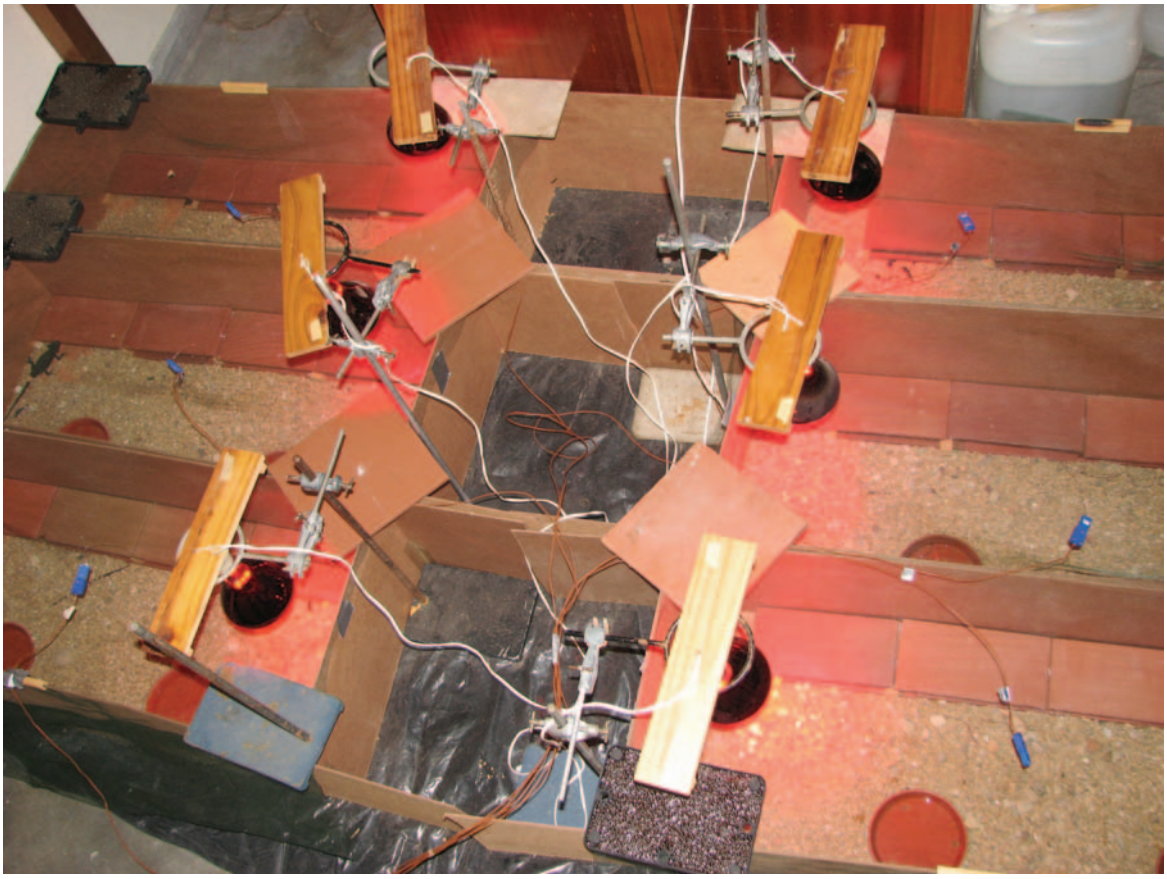

Figure 1. Thermal gradient setup used in determining the preferred body temperature of *Pseudocordylus capensis*. Each terrarium had an infrared lamp suspended above one end, providing each individual with a thermal gradient ranging from 50°C to 20°C.

1700 to ensure that the thermocouples were still in place and that the lizards were not entangled in the wires. Only T_bs recorded between 0900 and 1700 were used in analyses.

As I was interested in T_{pref} of the species and there was no significant difference in body temperature between individuals, the data were pooled. Data were normally distributed (Shapiro-Wilk's test) and T_{pref} was determined as the mean T_b, as well as the upper and lower set-points calculated as the bounds of the central 50% (Hertz *et al*. 1993) and 80% (Bauwens *et al*. 1995.) of the observed T_bs.

4.2.5 Habitat thermal quality

To determine whether the size of the rock formation plays a role in the activity pattern of *P. capensis* in a warm area, I compared the thermal quality of habitats available on small rocks to those available on large rock formations. I followed the method described by Hertz *et al*. (1993) to determine the mean thermal quality of the habitat (mean d_e) by calculating the average deviation of T_e from T_{pref}. I used T_{pref} determined as the mean T_b, with the upper and lower set-points calculated as the bounds of the central 80% (Bauwens *et al*. 1995.) of the observed T_bs for calculations of habitat thermal quality. When T_e was below the set-point range, d_e was calculated as the difference between T_e and the lower boundary of T_{pref}. When T_e was above the set-point range, d_e was calculated as the difference between T_e and the upper boundary of T_{pref}. When T_e was within T_{pref}, the d_e was equalled to zero. A low average d_e value indicated a good match between T_e and T_{pref}, therefore predicting a habitat where little or no thermoregulation may be required to maintain T_{pref}. A high average d_e value indicated a mismatch, and therefore predicting that some thermoregulatory effort will be needed to maintain T_b within the T_{pref} range with few optimal T_es available. Only data for clear days when the maximum ambient temperatures reached 25°C or higher, were included in the analyses.

4.2.6 Positional shifts

I investigated shifts in microhabitat use in *P. capensis* occurring in a ravine for four days in February (late summer, hottest month) and two days in October (mid-spring, cooler month) 2008. Two to three observers recorded active lizards between 07:30 and 18:00 and plotted their positions on a photograph of the ravine. I compared the percentage of lizard observed within and outside the ravine across seasons.

4.3 RESULTS

4.3.1 Daily activity patterns

Environmental conditions --- The environmental conditions for the two days in March 2006 were very similar, but varied from the conditions recorded for the day in January 2007. Temperature and relative humidity showed a significant difference between the days in March and the one in January (temperature: $F = 13.78$, df = 2, $P < 0.001$; relative humidity: $F = 15.20$, df = 2, $P < 0.001$), with January being warmer and more humid. No significant difference were observed for solar radiation ($F = 1.43$, df = 2, $P = 0.209$), UV-B ($F = 1.70$, df = 2, $P = 0.202$), and wind speed ($F = 1.59$, df = 2, $P = 0.222$). Wind speed did not show a consistent pattern and varied among the three days, with 14 March and 24 January showing an increase in wind speed as the day progressed, while wind speed was more or less constant on 15 March.

Activity patterns --- Data for the three days were analyzed separately as environmental conditions as well as activity of the species varied between the different days. Both *P. capensis* and *C. oelofseni* individuals were active throughout the daily observation periods, from 0800 when observations commenced, until 1800 when observations ended. Only in January did activity cease earlier (1600 for *C. oelofseni*, and 1700 for *P. capensis*) (Fig. 2). For this particular day, there was a negative correlation

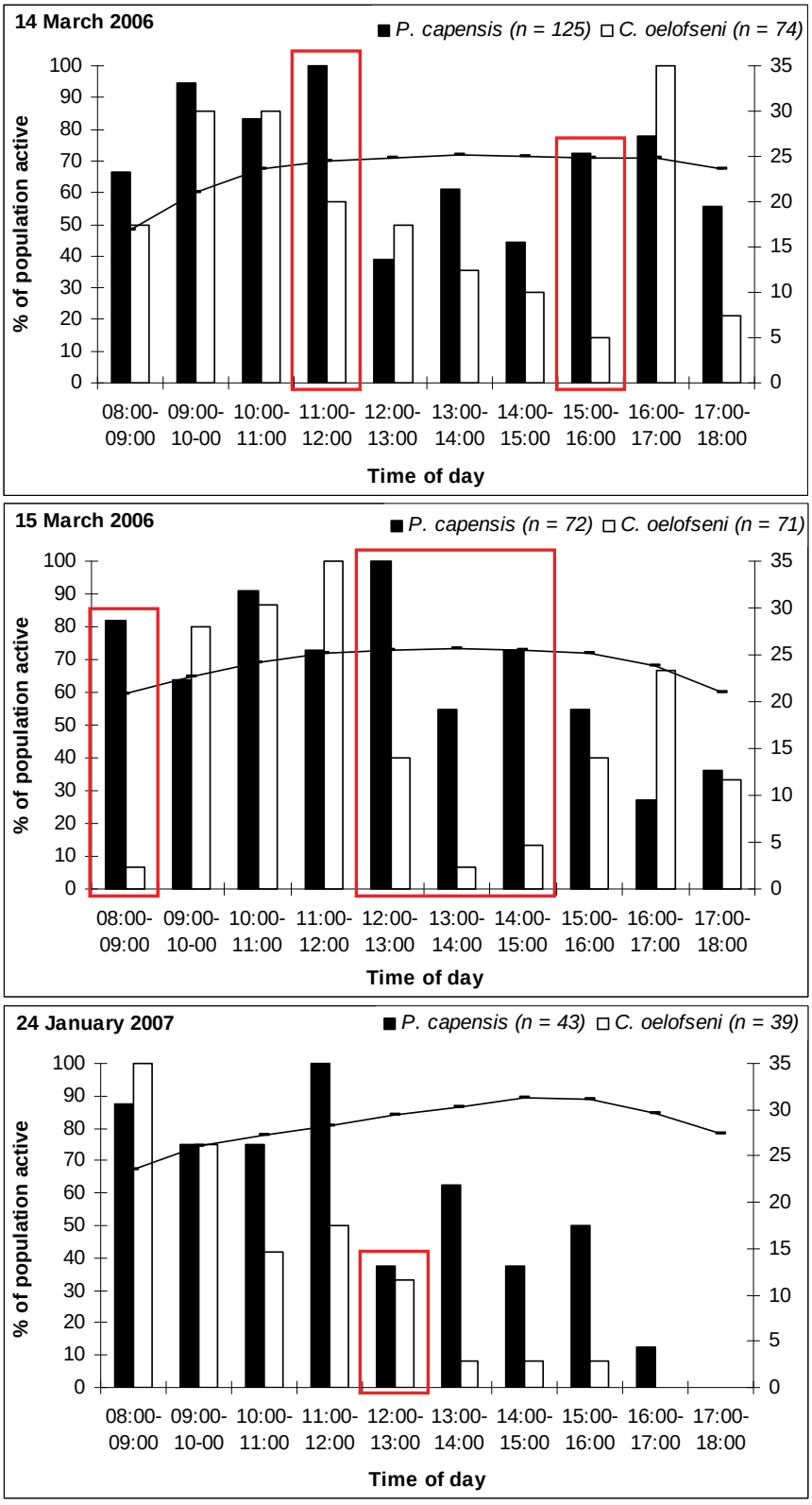

Figure 2. Daily activity patterns of *Pseudocordylus capensis* and *Cordylus oelofseni* recorded for three days in summer at Landdroskop. Ambient temperatures are indicated by the line. Significant differences in the proportion of the population active are indicated.

between the activity of *C. oelofseni* and temperature (correlation $r = -0.841$, $P < 0.05$) and wind speed (correlation $r = -0.953$, $P < 0.001$), and the activity of *P. capensis* and wind speed (correlation $r = -0.812$, $P < 0.05$).

Activity in the *P. capensis* population did not seem to follow a definite pattern, but fluctuated throughout the day between higher and lower activity levels on an hourly basis (Fig. 2). Peak activity was usually in the morning, with a slight decrease in activity in the afternoon. The *C. oelofseni* population followed a bimodal activity pattern (March) (Fig. 2), with peak activity in the early morning, a decrease in activity in the afternoon (Jan & March), and an increase in activity again in the late afternoon (March). Significant differences in the proportion of each population active during the afternoon hours were observed on all three days (Fig. 2). On 14 March there was a significantly larger proportion of the *P. capensis* population active between 1100 and 1200 ($z = 2.627$, $P < 0.01$), and between 1500 and 1600 ($z = 2.899$, $P < 0.01$) than the *C. oelofseni* population. On 15 March there was a significantly larger proportion of the *P. capensis* population active between 0800 and 0900 ($z = 3.481$, $P < 0.001$), and again between 1200 and 1500 (1200-1300: $z = 2.760$, $P < 0.01$; 1300-1400: $z = 2.267$, $P < 0.05$; 1400-1500: $z = 2.668$, $P < 0.01$). On 24 January there was a significant difference in activity among the two species between 1300 and 1400 ($z = 2.094$, $P < 0.05$), although the difference between 1100 and 1200 was only slightly non-significant ($z = 1.892$, $P = 0.058$). In general, a larger proportion of *P. capensis* individuals was active during the warm parts of the day than *C. oelofseni* individuals.

Rock and perch height --- It was previously reported that *P. capensis* selected significantly higher rocks and also perched significantly higher than the other melanistic cordylid species (Chapter 3). This was confirmed here, as *P. capensis* on average selected significantly higher rocks ($P < 0.001$ for all three days), and also perched significantly

higher ($P < 0.001$ for all three days) than *C. oelofseni*. When I compared rock and perch height across days, *P. capensis* selected significantly higher rocks and perches in January than in March (rock height: $F = 11.64$, df = 27, $P < 0.001$; perch height: $F = 5.05$, df = 27, $P < 0.05$) (Fig. 3). *Cordylus oelofseni* also selected significantly higher rocks in January ($F = 16.19$, df = 25, $P < 0.001$), but there was no significant difference in perch height across the three days ($F = 0.09$, df = 25, $P = 0.914$) (Fig. 3). In general, individuals of both species would perch on top of the rock or near the top of the rock early in the morning and again in the late afternoon (Fig. 3). During the afternoon *P. capensis* perched significantly lower than the height of the rock formation it was observed on (14 March 2006: t = 4.01, df = 10, $P < 0.05$; 15 March 2006: t = 6.15, df = 10, $P < 0.001$; 24 January 2007: t = 3.21, df = 8, $P < 0.05$). This was especially so in January (Fig. 3), the day for which the warmest temperatures where recorded (average of 31.25°C between 14:00 and 15:00). Perch height of *C. oelofseni* did not differ significantly from rock height during March (14 March 2006: t = 1.36, df = 10, $P = 0.203$; 15 March 2006: t = 0.42, df = 10, $P = 0.686$), but it did differ significantly in January (T = 26.00, $P < 0.05$), also most notably in the afternoon (Fig. 3).

Sun exposure --- In March 2006, the majority (75 - 80%) of the *P. capensis* population was recorded in the sun (Fig. 4). In the early morning lizards were only observed in the sun, but in the late morning and afternoon, a large percentage of the active population were also observed in shade and partial shade. This was especially so between 1300 and 1400, when 45 – 66% of the population were found in shady areas. A large percentage of the *C. oelofseni* population (70 – 75 %) were also observed in the sun, although they also selected shady areas in the afternoon (Fig. 4). In January, *P. capensis* was only observed in the sun between 0800 and 1200. Only about 30% of the population spent time in the sun, and the rest in shade (44.19 %) and partial shade (25.58 %). About

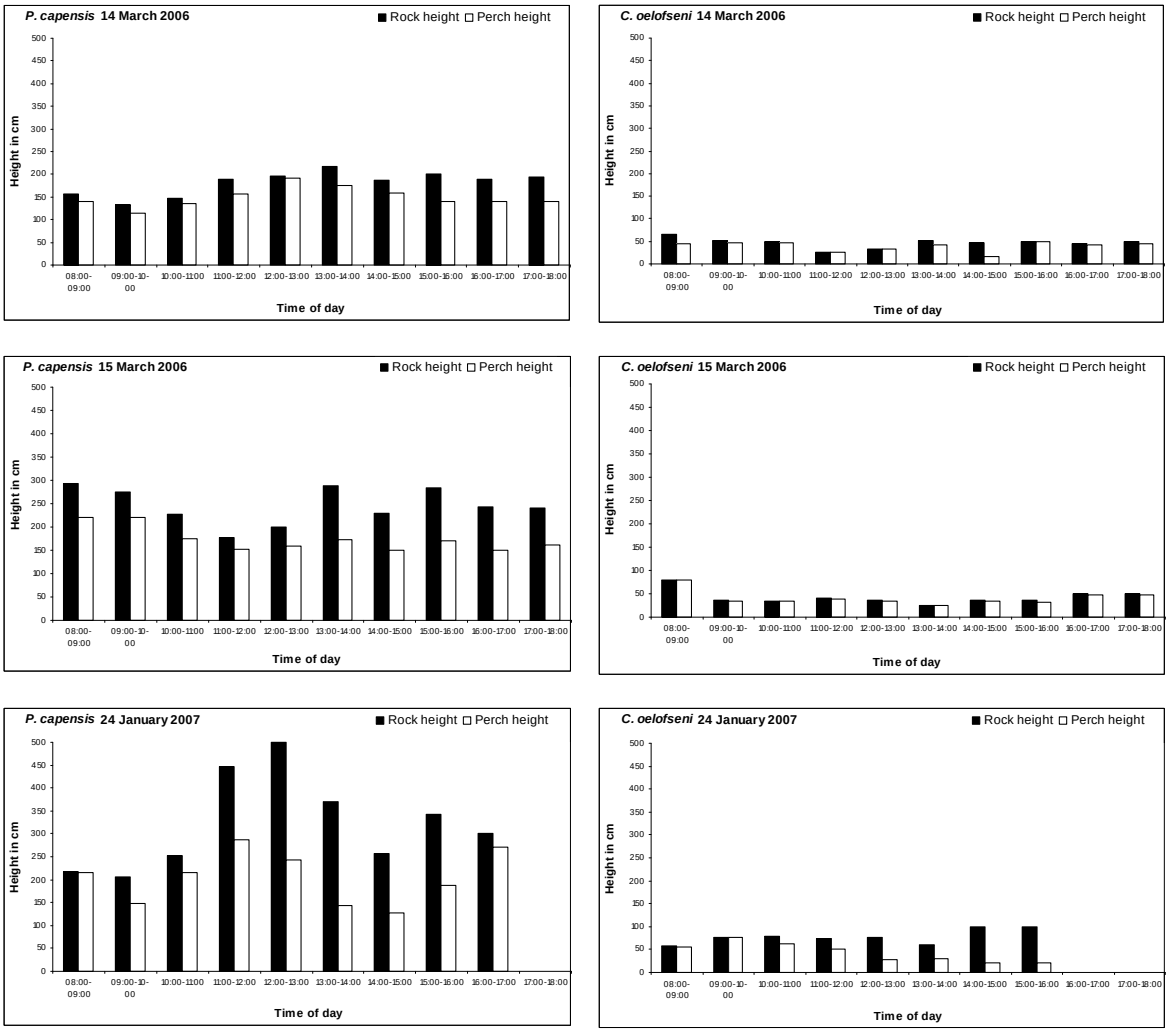

Figure 3. Rock and perch height selected by *P. capensis* (left) and *C. oelofseni* (right). All measurements were recorded at Landdroskop.

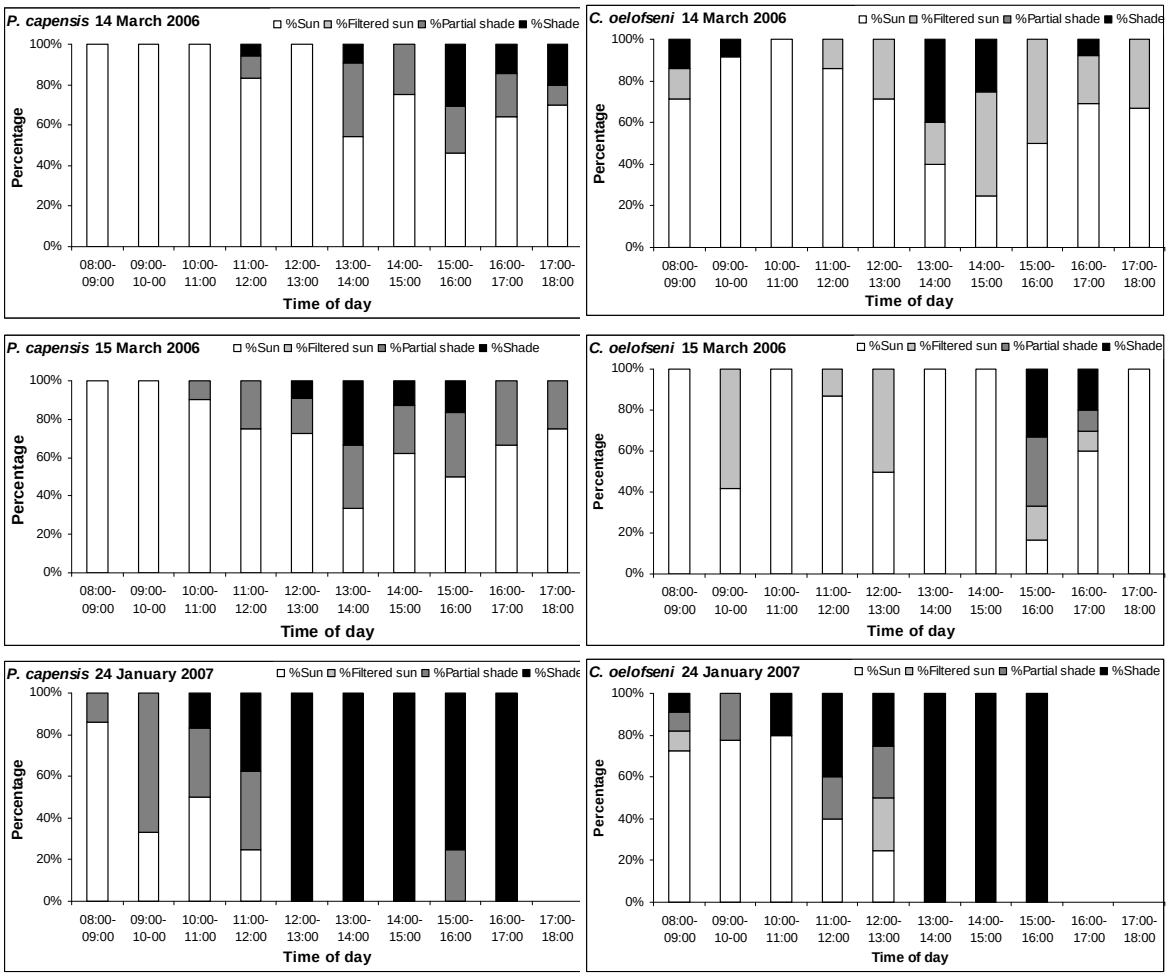

Figure 4. Percentage of *Pseudocordylus capensis* (left) and *Cordylus oelofseni* (right) observed in sun and shade.

60% of the *C. oelofseni* population was observed in the sun until 1300, after which they were only observed in shade.

It would appear that both species start moving from sunny areas to more shady areas when air temperature reaches a value of about 23°C. On warmer days when air temperatures reach high values early in the day, they only spent a limited time in the sun, and the rest in shade.

4.3.2 Preferred body temperature

Mean T_{pref} for *P. capensis* was 30.04°C ± 1.34°C with the central 50% of body temperatures measured between 27.84°C and 32.04°C, and the central 80% measured between 26.50°C and 32.99°C. This is within the range recorded for other cordylid species (Table 1).

4.3.3 Habitat thermal quality

For those days where the ambient temperature exceeded 25°C, the thermal habitat provided by large rock formations was more suitable than the thermal habitat provided by small rock formations for *P. capensis* (Z = -2.38, $P < 0.05$). The average deviation of T_e from T_p (= d_e, Table 2a) for large rock formations was 4.02°C, while the average deviation for small rocks was 5.35°C. In contrast to large rock formations where 21.70% of all T_es were above T_{pref}, 42.67% of T_es on small rocks were above T_{pref} (Table 2b, Figure 5, 6). The north- and south-facing slopes of large rock formations also differed, with the north-facing side being slightly more suitable than the south-facing side where the T_e was often below T_{pref} (Table 1b).

The daily pattern of d_e for warm days indicated that the thermal environment of small rocks improved quickly from 0700 to 1100 on the north-facing side and to 1200 on

Table 1. Summary of preferred body temperatures for cordylid lizards.

Species	**T_{pref} (mean) ± SE (°C)**	**Reference**
Pseudocordylus capensis	30.04 ± 1.34	This study
Cordylus cataphractus	29.84 ± 0.05	Truter 2009
Cordylus cordylus	32.1 ± 0.7	Clusella Trullas 2009
Cordylus niger	32.6 ± 0.3	Clusella Trullas 2009
Cordylus oelofseni	33.6 ± 0.3	Clusella Trullas 2009
Cordylus polyzonus	33.6 ± 0.3	Clusella Trullas 2009
Cordylus jonesi	33.5 ± 0.3	Wheeler 1986
Cordylus vittifer	32.1 ± 1.8	Skinner 1991
Platysaurus intermedius wilhelmi	31.5 ± 1.7	Lailvaux *et al*. 2003

Table 2. Summary of the thermal quality of the habitat (d_e) for *P. capensis*. Average d_es for the various microsites on small and large rock formations ± SE (a), and percentages of T_e below, within and above T_p (b) are shown.

	Large rock formation – south-facing				**Large rock formation – north-facing**				**Total large rock formation**	**Small rock formation**		**Total small rock formation**
(a)	**Bottom**	**Middle**	**Top**	**South-facing**	**Bottom**	**Middle**	**Top**	**North-facing**		**South-facing**	**North-facing**	
d_e index	2.30 ± 1.24	3.06 ± 1.41	3.76 ± 1.42	3.04 ± 0.77	6.48 ± 1.42	5.53 ± 0.89	2.95 ± 0.96	4.99 ± 0.68	4.02 ± 0.52	6.50 ± 1.67	4.21 ± 1.89	5.35 ± 1.25
(b)												
T_e below T_{sel}	49.38	43.52	53.70	49.18	82.25	90.12	73.77	82.05	66.08	27.78	64.66	46.22
T_e within T_{sel}	6.79	25.74	16.36	15.74	2.62	7.41	16.67	8.90	12.22	8.02	14.20	11.11
T_e above T_{sel}	43.83	30.74	29.94	35.08	15.12	2.47	9.57	9.05	21.70	64.20	21.14	42.67

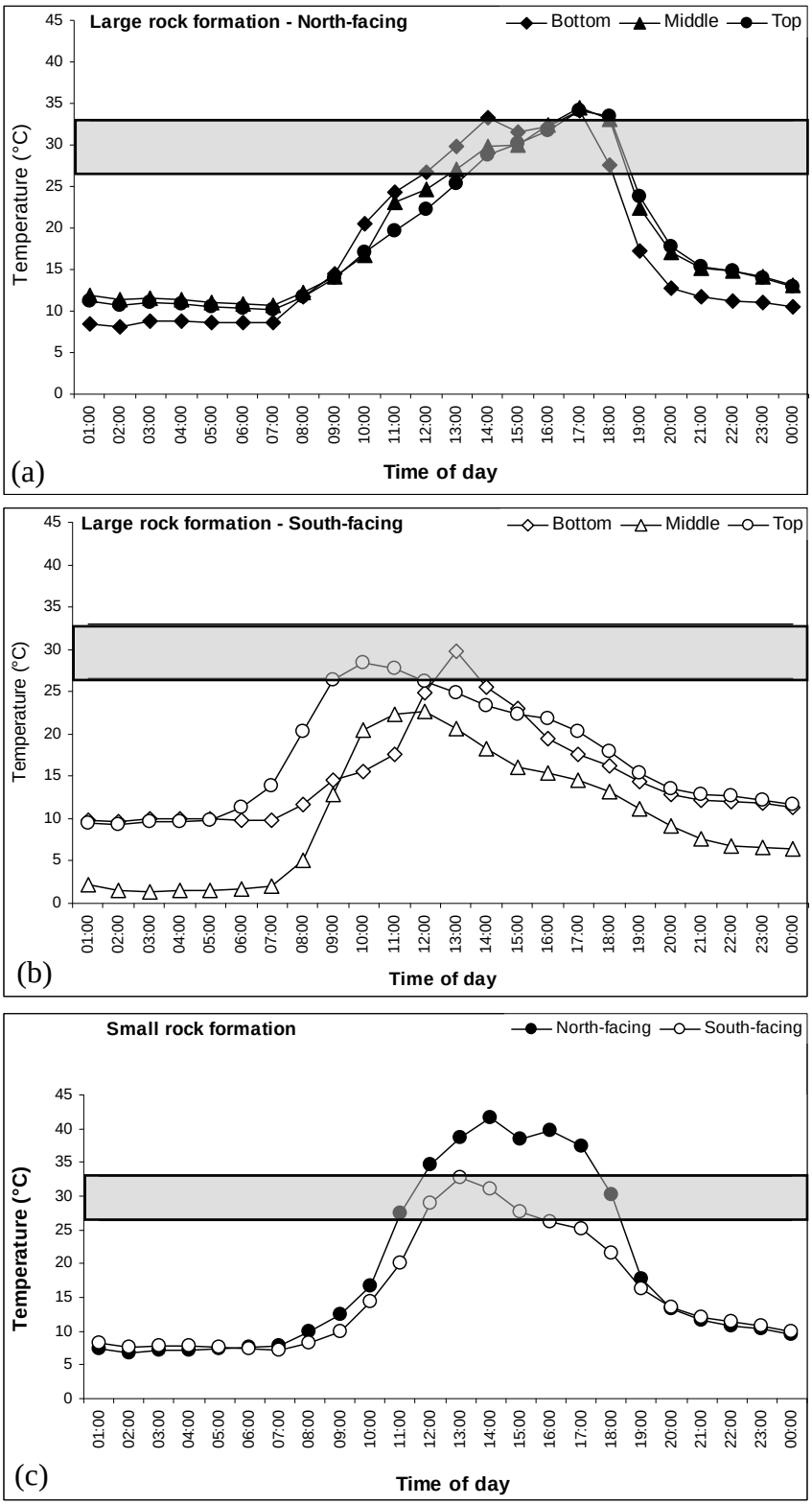

Figure 5. Available T_es for *Pseudocordylus capensis* on the northern (a) and southern side (b) of a large boulder > 2m in height, and (c) a small rock < 0.5m in height. The range of T_p is indicated by the shaded area.

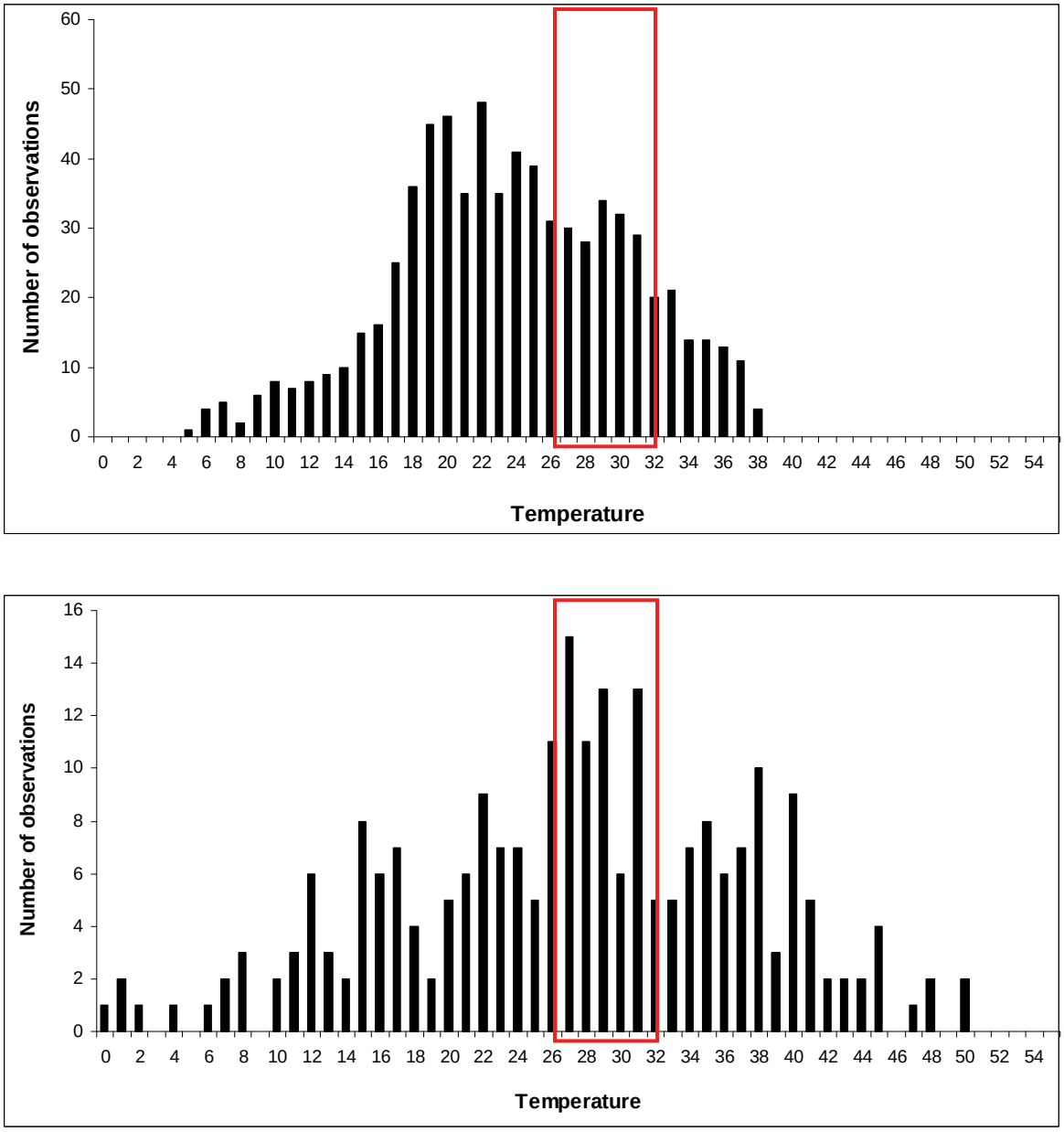

Figure 6. Distributions of daily T_e available to *Pseudocordylus capensis* on large (top) and small (bottom) rock formations. Vertical rectangles indicate the central 80% of body temperatures selected in a thermal gradient.

the south-facing side (Fig. 7). Between 1100 and 1600 the north-facing side experienced a sharp decline in d_e, with an improvement again between 1600 and 1800. The south-facing side experienced a slight decline in d_e between 1300 and 1500 and again from 1600 onward. On large rock formations, the north-facing side experienced a quick improvement in d_e between 0700 and 1200, with a sharp decline from 1800 at the bottom, an improvement between 0700 and 1400, with a sharp decline from 1800 in the middle, and an improvement between 0700 and 1500, with a decline from 1800 (Fig. 7). On the south-facing side, d_e improved quickly between 0700 and 1300 at the bottom, 0700 and 1200 in the middle, and 0500 and 0900 at the top. Thermal quality declined in the bottom region of the rocks from 1200, between 1600 and 1700, and from 1800 in the middle region, and from 1600 in the top region (Fig. 7).

4.3.4 Positional shifts

The different slopes of the ravine are explained in Figure 8. In February and October, the ravine received no sun early in the morning due to the large shadow cast by the eastern ridge. From midmorning to late afternoon, the north-facing slope experienced full sun, with only areas underneath overhangs providing shade. The eastern ridge of the ravine received sun from late morning until late afternoon. The south-facing slope only received sun in the afternoon, with some areas never receiving any sun. Although no T_es were recorded, based on sun exposure, the north-facing slope was classified as the warmer side and the south-facing slope as the cooler side of the ravine. Lizards on the north-facing slope were active early in the morning (0737), but all activity ceased on this side during the afternoon, with some individuals becoming active again only late in the afternoon because this area was still exposed to solar radiation. Lizards on the east- and south-facing slopes of the ravine became active around 1100 and remained active until late in the afternoon.

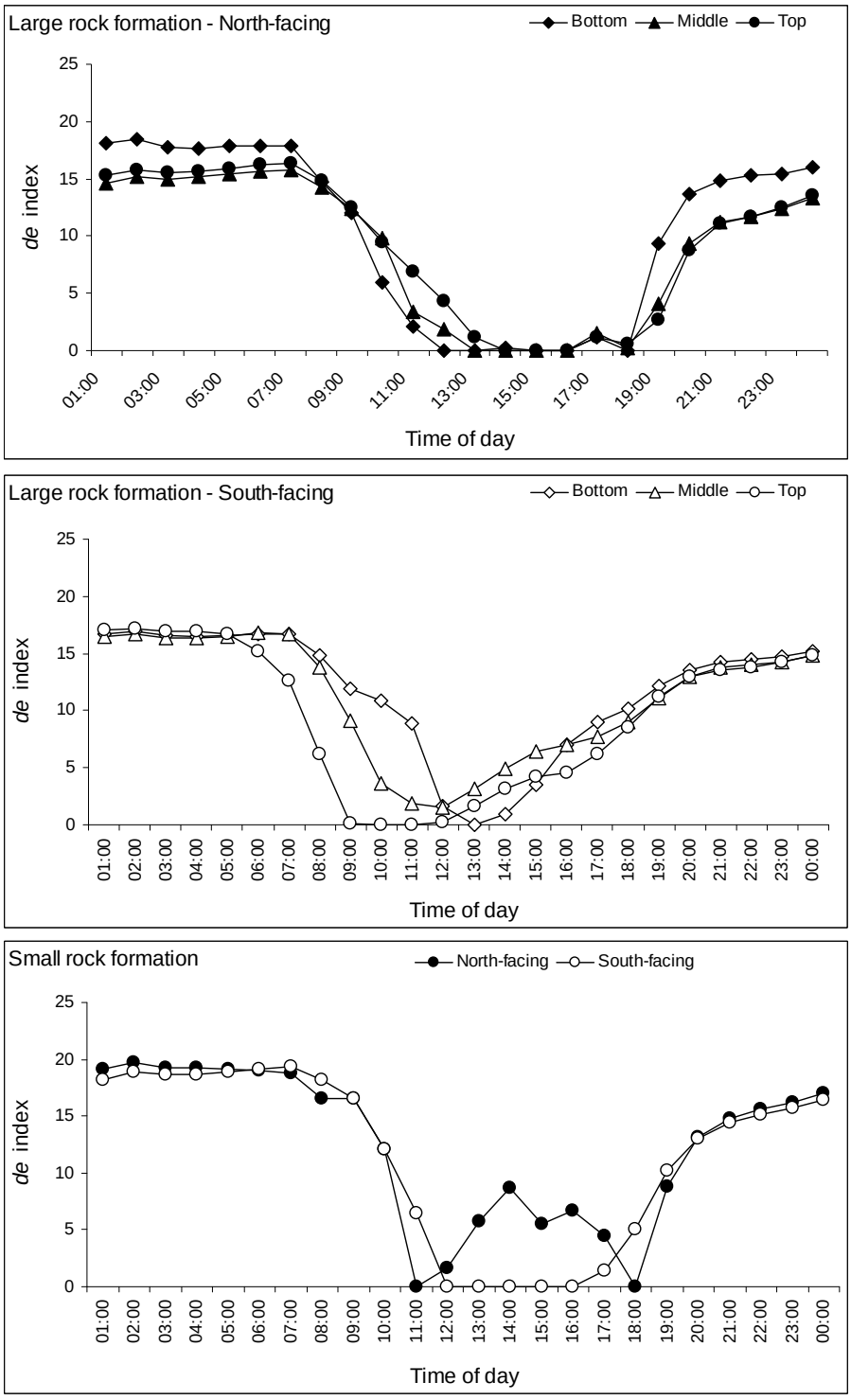

Figure 7. Daily pattern of thermal quality of the habitat (d_e index) for *P. capensis* at the different microsites on the northern (a) and southern sides (b) of a large and small (c) rock formations. Values are the means gathered hourly for three hot days ± SE.

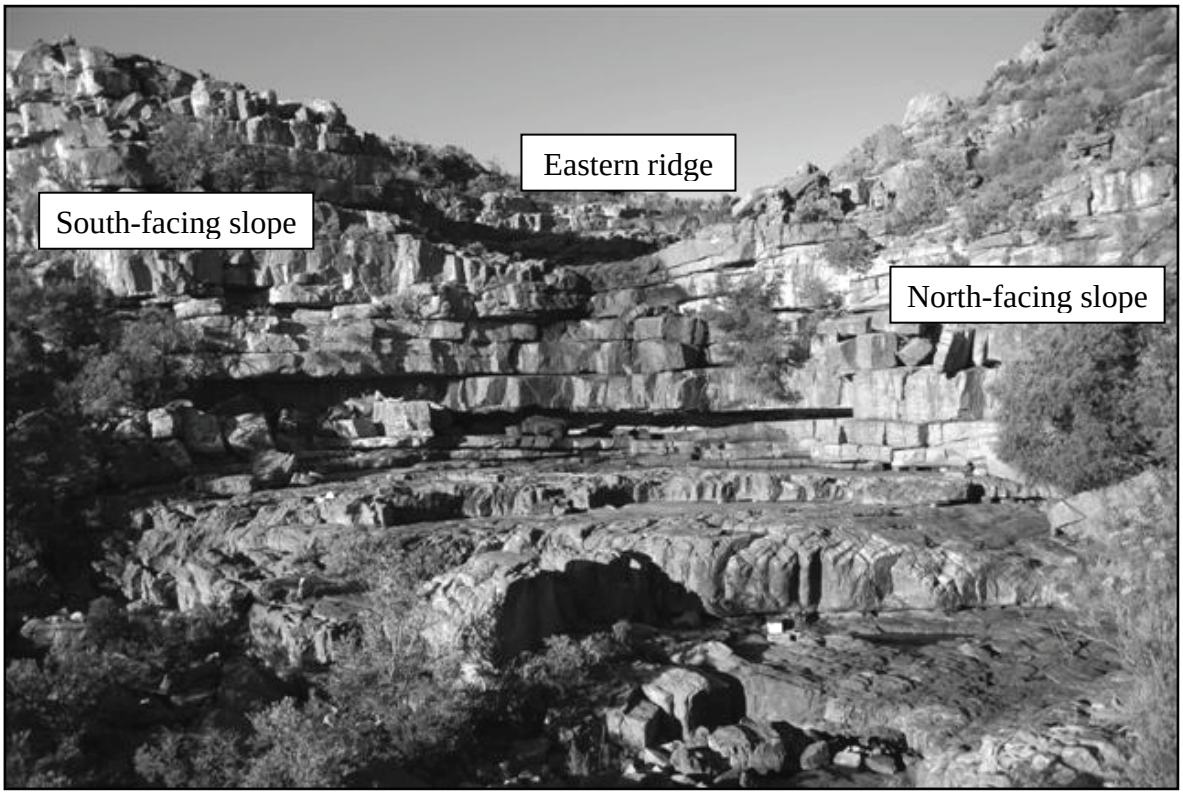

Figure 8. The ravine at the Gifberg study area.

During February, 98% of all observations were recorded within the ravine, with 49% of observations made on the north-facing slope and 51% on the south-facing slope. In October, 90% of all observations were recorded within the ravine, with 56% of observations made on the north-facing slope and only 44% on the south-facing slope. It was also noted that lizards on the south-facing slope concentrated their movements in the central and lower parts of the ravine during February (summer) and in the central and upper parts during October (spring).

4.4 **DISCUSSION**

With this study I attempted to obtain information on aspects of the thermal biology of the melanistic species, *Pseudocordylus capensis*, in order to eventually understand the causal factors associated with habitat selection. Results confirmed that surface activity differed from other cordylids occupying relatively small rocks, that the mean thermal quality index for *P. capensis* is higher with T_es matching T_{pref} for longer periods in the large rock habitat and that seasonal habitat shifts (among sun facing slopes) may occur.

The preferred body temperature, as determined by laboratory studies in a setup with few constraints for selecting ideal environmental temperatures, for *P. capensis* was 30.04 ± 1.34°C, which is within the range reported for cordylid lizards (see Clusella-Trullas, *et al*. 2007b). The limited interspecific variation in T_{pref} among cordylids suggests some conservatism in this trait. However, the possibility exists that in a wide-spread species like *P. capensis*, the T_{pref} may show plasticity between locations. Rodrígues-Serrano *et al*. (2009) reported flexibility in the thermal physiology of *Liolaemus* lizards, and concluded that this plasticity played a role in this species colonising a wide array of thermal environments. Correlated variation in T_{pref} will reduce the differentials between T_es and T_{pref}s and limit the costs of thermoregulation in extreme situations. On the other hand, free

movement among thermal patches (behavioural adjustments) along with a larger body size could make life possible in a relative warm environment for a melanistic lizard, even though T_{pref} is relative low.

Results show that there were significant differences in the daily activity patterns of two melanistic cordylid species, *Cordylus oelofseni* associated with small rock formations and *P. capensis* associated with large rock formations. *Cordylus oelofseni* exhibited a bimodal pattern in summer, active mainly in the morning and, depending on climatic conditions, also in the late afternoon, whereas a large percentage of the *P. capensis* population was active throughout the day. Not only on hot days, but also on cooler, windy days, more *P. capensis* than *C. oelofseni* individuals were active during the warmest part of the day. The difference in activity pattern between *P. capensis* and *C. oelofseni*, suggests that a more mobile melanistic lizard (*P. capensis*) can increase its activity time by utilizing the greater diversity of thermal microhabitats available on large rock formations.

Clusella Trullas *et al*. (2009) reported the thermal quality of the habitat for *C. oelofseni* to be moderately suitable during summer with a d_e of 4.4°C and 72.3% of the T_es below T_{pref}. However, nearly 21% of all T_es were above T_{pref}, with the thermal habitat being most suitable between 1400 and 1600 (Clusella Trullas *et al*. 2009). The bimodal activity pattern of *C. oeloefseni* observed in this study was therefore not surprising, and suggests that the available T_es during the middle of the day was too high ($T_e > T_{pref}$), thus restricting lizard activity. This was confirmed by the thermal quality index for *P. capensis* calculated for the small rock habitat, inhabited by *C. oelofseni*. The thermal quality index for *P. capensis* suggested a match between T_e and T_{pref} for 7 hours in the small rock environment, that is, if the lizards inhabiting the small rocks move between aspects (north to south).

In the large rock habitat the average thermal quality index for *P. capensis* was more favorable (lower % of T_es > T_{pref}) and the activity period matching T_es with T_{pref} extended to 9 hours. I therefore confirm that in summer large rock formations provided increased thermal opportunities to the melanistic *P. capensis*. The larger rock faces provide less chance for overheating (T_es >T_{pref}). Shifting between microhabitats has also been reported for other lizards. For example, the herbivorous lizard, *Cnemidophorus murinus*, extends its activity period by shifting between appropriate microhabitats in order to maintain high T_bs for the entire day, rather than increasing its T_b (Vitt *et al*. 2005).

From behavioural observations it was clear that *P. capensis* makes use of the vertical aspect of the large boulders and vertical cliffs by shuttling between perches of different elevations during the day. In the early morning the majority of the *P. capensis* population was observed on top or near the top of rock formations. During the warmer parts of the day, lizards moved to lower perches and were often observed more or less in the mid-levels of the rock formation where the thermal quality of the habitat was better and often close to T_{pref}. Elevated perches are usually cooler than ground level perches due to a decrease in air temperature and an increase in wind speed (Geiger 1965; Stevenson 1985; Adolph 1990). On warmer days, *P. capensis* also selected higher rock formations and perched at higher levels, indicating the importance of vertical movement in a warm environment. In the cooler montane environment the small rock formations were found to be thermally more suitable for *C. oelofseni*, possibly due to the smaller size of this species. *Cordylus oelofseni* also selected slightly higher rock formations on warmer days, but the morphology of this species excludes it from large vertical movement on large rock formations.

It has been reported that in warm areas where environmental temperatures may be too hot for lizards to be active, the animals restrict their activity to the cooler parts of the day or areas with low ambient temperatures (Huey & Slatkin 1976; Hertz & Huey 1981;

Angert *et al*. 2002; Ibrahim, 2002). *Anolis cybotes* actually avoids sunny perches and basks infrequently, which led to the suggestion that if a habitat in a relatively shaded area is thermally suitable, basking may not be necessary (Hertz & Huey 1981). Under the cost-benefit model, Huey & Slatkin (1976) predicted thermoconformity if precise thermoregulation is too costly (time spent shuttling). However, studies by Brown & Weatherhead (2000), Blouin-Demers & Weatherhead (2001) and Row & Blouin-Demers (2006) suggested that the Huey & Slatkin (1976) model may not be valid for reptiles living in extreme environments (in their case, close to the cold northern limits of these species distribution). In these cold environments, it seems that when the thermal quality was low, thermoregulation was more effective, as long as T_es are available to obtain T_{pref}. The importance of factors such as the spatial distribution of operative temperatures (T_es) in the habitat (biophysical environment) is emphasized. Brown & Weatherhead (2000) showed that the availibity of T_es within the T_{pref} range would lower the cost of thermoregulation and it is expected that the cost of thermoregulation will be substantially reduced by a thermal mosaic (Huey 1974; Huey & Slatkin 1976), which is produced by dense vegetation cover near ground level (Strijbosch 1988; Díaz & Carrascal 1991) or rough near-vertical rock faces in large rocks. The majority of *P. capensis* individuals were observed in shaded areas, especially in the afternoon, and I am of the opinion that the large rock formations retain their heat well and long enough so that shaded habitats provide these lizards with good thermal opportunities. In *P. capensis* it would appear that, while there is a high cost involved in utilizing the diversity of thermal habitats available on large rocks, the benefits are good, thus enabling this melanistic species to survive in warm environments. The possibility that the preference for large rocks could be predator avoidance cannot be excluded, but currently I have no data to assess this scenario.

The limited habitat shift in *P. capensis* occurring in a ravine set-up suggests that the ravine provides a suitable area for occupation throughout the year. However, during the cooler season a slightly larger number of observations were made on the north-facing side of the ravine. The north-facing side of the ravine received sun from early morning till late afternoon throughout the year, while the south-facing side only received sun from late morning, with some areas never receiving sun. Although still found inside the ravine, the lizards on the southern side seem to shift their habits slightly upward during the cooler time of the year. Land iguanas of Galapagos have been shown to occur on the cooler windy plateau during summer, but during winter, they move to the sunny cliff faces (Christian *et al*. 1983). The green anole, *Anolis carolinensis*, also shifts habitats and during winter, individuals aggregate on a south-facing bluff (Bishop & Echternacht 2004). The restriction of *P. capensis* to large rocks in warm areas (Chapter 3), confirm that the biophysical properties of these structures play an important part in habitat selection. Seasonal shifts in habitat selection to ensure suitable retreat sites (Webb & Shine, 1998) but also guaranteed solar exposure may explain the habitat shifts observed for *P. capensis* during winter months.

In summary, *Pseudocordylus capensis* displayed behavioural adjustments living on large rock faces in warm and cold areas. By selecting thermally suitable microsites (high thermal quality) in a vertical gradient on a large rock formation, this species is able to increase its daily activity period, and escape the restriction of overheating in a relative warm environment. Larger rocks provided a large range of possible T_es close to T_{pref} and on average a lower thermal quality index for the melanistic *P. capensis*. Seasonal habitat shifts to ensure thermal suitable habitats confirms the important role of biophysical aspects to compensate for extreme differential among T_{pref} and T_es. However, since I did not measure body temperatures in free-living field lizards, I do not have information on

thermoregulatory effectiveness and therefore an indication of costs involved in the thermobiology of this melanistic species living in a relative warm environment.

CHAPTER 5

THE ROLE OF PREDATORS AND ENVIRONMENT IN SHAPING BODY ARMOUR IN MELANISTIC CORDYLID LIZARDS

5.1 INTRODUCTION

The Cordylidae is a family of lizards endemic to Africa. All are heliothermic baskers (Mouton & Van Wyk 1997; Branch 1998), the majority are rock-dwellers (Mouton & Van Wyk 1997; Branch 1998), and all species studied to date are ambush foragers (Cooper, Whiting & Van Wyk 1997; Mouton & Van Wyk 1997; Mouton, Geertsema & Visagie 2000; Du Toit *et al*. 2002; Chapter 6). The predators of rock-dwelling cordylids can probably be partitioned into two categories, namely aerial predators and terrestrial predators (Mouton & Flemming 2001). During activity, rock-dwelling cordylids spend considerable time on rock perches, basking and scanning the environment for food. Perching rock-dwelling cordylids will be particularly visible to birds of prey, which are highly visually orientated. The majority of these predators only hunt by day and would be unable to extract prey from crevices. Besides crypsis, a speedy retreat to their rock shelters will be the most effective way for perching cordylids to avoid capture by these predators. Terrestrial predators (i.e. snakes and mammals), on the other hand, use auditory, olfactory and visual cues to locate prey (Bittner 2003) and would in many cases be able to extract lizards from their shelters. Many are also nocturnal and can prey on lizards when the lizards are inactive in their shelters. Speed will be ineffective as the lizards will either be too cold to run, or will have no place to run to. Well-developed armour and mechanisms to prevent extraction from crevices would be required.

It is clear that the two categories of predators will have opposing morphological demands on the lizards, aerial predators demanding speed and terrestrial predators armour. Degree of armour and running speed are, however, negatively correlated in cordylids (Losos *et al*. 2002) and one would expect that the morphology of a species would be dictated by the relative impacts of the two categories of predators. Rock-dwelling species spending considerable time in the open where they are exposed to aerial predators should be relatively fast and should have relatively little armour. Those species spending most of their activity time in less exposed positions, on the other hand, should have a higher degree of armour as the impact of terrestrial predators (demanding armour) will be larger than the impact of birds of prey (demanding speed).

At least eight melanistic cordylid species occur in the south-western districts of South Africa (Mouton 1985, 1986a, 1986b; Mouton & Oelofsen 1988; Mouton & Van Wyk 1995; Daniels, Mouton & Du Toit 2004). The association of most melanistic cordylids with cool coastal and montane localities (Janse van Rensburg, Mouton & Van Niekerk 2009; Chapter 2) is in agreement with the thermal melanism hypothesis which states that under conditions of low temperature, dark individuals have an advantage over light individuals because they heat up faster at a given level of solar radiation (Norris1967; Kettlewell 1973; Luke 1989; Clusella Trullas, Van Wyk & Spotila 2007a). Melanism in cordylids is believed to have evolved during the Miocene (17-9 Ma ago) (Daniels *et al*. 2004; Janse van Rensburg *et al*. 2009; Chapter 2), a period characterized by major climatic changes as well as the formation of a permanent southern polar ice cap between 16.5-14 Ma ago (Woodruff, Savin & Douglas 1981). One can assume that during the evolution of melanism in cold environments, the lizards would have spent more time basking and would accordingly have been more exposed to aerial predation than would have been the case in warm environments. This assumption is based on

observations for several other lizard species where highland populations spent more time basking in the open than lowland populations (Van Damme *et al*. 1989; Van Damme, Bauwens & Verheyen 1990).

The aim of my study was to investigate the degree of body armour in closely related melanistic and non-melanistic cordylid species. I predicted that melanistic cordylid species will be less armoured than closely related non-melanistic species. I also predicted that melanistic species with a low degree of spinosity and lesser developed osteoderms will venture further from their shelters than those displaying a high degree of spinosity and well-developed osteoderms.

The melanistic cordylid species are found in four clades (Frost *et al*. 2001), allowing for direct comparisons between closely-related melanistic and non-melanistic species. The *cordylus-niger-oelofseni* complex consists of two melanistic species, *Cordylus niger* and *C. oelofseni*, and a non-melanistic species, *C. cordylus*, whereas *Cordylus polyzonus* consists of both melanistic and non-melanistic populations. The closest non-melanistic relative of *C. peersi* (melanistic) is currently regarded as *C. lawrenci* (Frost *et al*. 2001), although follow-up studies are needed to confirm this. The closest relative of the two melanistic sister species, *Pseudocordylus capensis* and *P. nebulosus*, is unclear at the moment, and for this reason we did not include a non-melanistic relative for comparisons in this clade. Unlike other melanistic cordylids, *P. capensis* has an extensive distribution, occurring from cool montane areas to warm lowland area (Janse van Rensburg *et al*. 2009; Chapter 2). In this study I also compared the degree of body armature between *P. capensis* populations in cool environments and those occurring in warm environments, expecting those in warm environments to be better armoured than those in cool environments.

5.2 MATERIALS AND METHODS

5.2.1 Spinosity and osteoderm index

Morphological variables related to body armour and escaping ability were collected for preserved adult specimens of the melanistic cordylid species and their closely-related non-melanistic species. Variables included snout-vent-length (SVL), several spine measurements and osteoderm indices. Spine length was measured at seven points on each specimen following Losos *et al*. (2002): tail, hindleg, side of the trunk, neck and three head spines, i.e. the longest spine directly anterior to the tympanum, the longest spine on the posterior margin of the head, and the longest spine on the side of the head posterior to the tympanum.

Skin sections were removed from the dorsal body of six melanistic and three non-melanistic cordylid species. I obtained skin sections from six specimens each of *Cordylus niger*, *C. oelofseni*, *C. cordylus*, *C. polyzonus* (melanistic), *C. polyzonus* (non-melanistic), *Pseudocordylus capensis* (warm northern locality), and *P. capensis* (cool southern locality). Skin sections from only three specimens of *P. nebulosus* were available for this study. This species is only known from a single locality (Mouton & Van Wyk 1995), and is listed as threatened (Baard *et al*. 1999). Since the phylogenetic relationship between *C. peersi* and *C. lawrenci* is still unclear (Frost *et al*. 2001), only one adult specimen of each were included in my sample. Each skin section included two rows of three scales in those species with normal scales, and a skin section of comparable size in those species with granular scales. Serial histological sections were cut at 10-12 µ and stained with hematoxylin and eosin. I measured the cross-sectional area of the osteoderm using the computer package Leica QWin Standard Version 2.3 (Leica Microsystems Imaging Solutions). I calculated an osteoderm index (OI) for each species by dividing the cross-sectional area of the osteoderm midway along the plate by the breadth of the osteoderm, or, in those species where the osteoderms are smaller than the

corresponding scales, by the breadth of the scale. I obtained 6-10 values for each individual and then used the mean as representative of the osteoderm index for each species.

5.2.2 Escape Distance

Data on the distance a lizard will run when a predator approaches, and the distance the lizard moves away from its crevice were recorded for five of the melanistic species. Distances moved by lizards were investigated in the field at Jacobsbaai for *C. niger* and melanistic *C. polyzonus*, at Piketberg, Dasklip Pass and Landdroskop for *C. oelofseni*, and at Landdroskop for *P. capensis* (southern population) and *P. nebulosus*. Once a lizard has been spotted, an observer walked towards it at a constant speed, simulating the approach of a predator. The distance the lizard moved until it entered a refuge was recorded. If a lizard did not enter a refuge, the observer continued to advance until it moved at least 5 m. Escape distance was the distance a lizard moved during the trail. No data were obtained for the northern population of *P. capensis* due to the fact that lizards basked at heights that were inapproachable by human observers. No data were recorded for *C. peersi* either, as no lizards were found to be active during my survey.

5.2.3 Statistical Analyses

Analysis of covariance (ANCOVA) was used to test for any differences in spine length between the melanistic and non-melanistic members in the different clades. To test for differences in osteoderm index, analysis of variance (ANOVA), followed by Scheffe's tests were used for the clades containing more than two species, and a *t*-test for the melanistic and non-melanistic *C. polyzonus* populations. Principal component analyses (PCA's) were used to investigate the degree of spinosity and osteoderm development in melanistic cordylids. To

remove the effects of differences in body size, each morphological variable was regressed against SVL. An ANOVA, followed by a Fisher LSD post hoc test, was used to investigate differences in the distance from the crevice and distance moved among the different species.

5.3 RESULTS

5.3.1 Spinosity

Spine lengths for the different species are summarized in Table 1. In the *cordylus-niger-oelofseni* clade, individuals of the non-melanistic species, *C. cordylus*, were significantly more spinose those of the two melanistic species (*C. niger* and *C. oelofseni*) ($F = 31.92$, df = 93, $P < 0.001$). *Cordylus cordylus* only did not differ significantly from *C. niger* in spine length on the front leg ($P = 0.771$), and from *C. oelofseni* in spine length on the posterior margin of the head ($P = 0.735$). There were no significant differences between *C. oelofseni* and *C. niger* in terms of tail, hind leg and neck spines (tail: $P = 0.999$; hind leg: $P = 0.976$; neck: $P = 0.305$), but *C. oelofseni* had significantly shorter spines than *C. niger* on the front leg, trunk and anterior to the tympanum ($P < 0.001$ for all cases).

Individuals in a non-melanistic *C. polyzonus* population were also more spinose than those in a melanistic population of *C. polyzonus* ($F = 15.58$, df = 26, $P < 0.001$). Only spines on the tail and anterior to the tympanum did not differ significantly (tail: $P = 0.917$; tympanum: $P = 0.507$). In contrast, *Cordylus peersi* was more spinose than its closest non-melanistic relative, *C. lawrenci*. *Cordylus peersi* had significantly longer spines than *C. lawrenci* ($F = 21.76$, df = 11, $P < 0.05$). Only neck spines did not differ significantly ($P = 0.415$).

Table 1. Summary of spine morphology of melanistic cordylid species and their closest non-melanistic relatives. Standard errors are indicated as ± SE. Melanistic species are indicated by *.

			Spine measurements (in mm)						
Species	***N***	**SVL**	**Tail**	**Hind leg**	**Front leg**	**Trunk**	**Neck**	**Tympanum**	**Post. Margin**
P. capensis (northern pop.)*	19	89.24 ± 2.37	3.09 ± 0.11	1.93 ± 0.08	1.77 ± 0.07	0	0	1.39 ± 0.07	0
P. capensis (southern pop.)*	19	93.41 ± 1.86	3.08 ± 0.11	2.27 ± 0.06	1.95 ± 0.08	0	0	1.55 ± 0.07	0
*P. nebulosus**	7	71.80 ± 1.28	3.2 ± 0.10	2.05 ± 0.04	1.88 ± 0.08	1.46 ± 0.07	1.27 ± 0.15	0.97 ± 0.07	0
*C. polyzonus**	19	99.02 ± 2.29	4.55 ± 0.20	2.65 ± 0.08	2.45 ± 0.09	0	2.39 ± 0.11	2.32 ± 0.11	2.43 ± 0.08
C. polyzonus	10	105.78 ± 3.51	4.57 ± 0.31	3.18 ± 0.16	2.88 ± 0.14	0	1.91 ± 0.12	2.53 ± 0.21	2.67 ± 0.08
*C. peersi**	10	76.49 ± 1.73	4.74 ± 0.20	3.14 ± 0.15	3.02 ± 0.14	3.60 ± 0.15	2.51 ± 0.08	2.18 ± 0.16	1.93 ± 0.13
C. lawrenci	4	59.39 ± 4.04	3.22 ± 0.19	2.33 ± 0.25	2.19 ± 0.21	2.29 ± 0.23	2.42 ± 0.12	1.60 ± 0.12	1.46 ± 0.14
*C. oelofseni**	42	60.36 ± 0.51	3.82 ± 0.08	2.17 ± 0.05	1.74 ± 0.03	2.13 ± 0.05	1.50 ± 0.04	1.22 ± 0.03	1.27 ± 0.03
*C. niger**	27	76.23 ± 1.39	3.82 ± 0.12	2.19 ± 0.07	2.04 ± 0.06	2.48 ± 0.07	1.63 ± 0.06	1.48 ± 0.06	1.54 ± 0.07
C. cordylus	28	74.12 ± 1.36	4.42 ± 0.13	2.43 ± 0.07	2.09 ± 0.07	2.80 ± 0.10	2.13 ± 0.08	1.66 ± 0.08	1.32 ± 0.06

Pseudocordylus capensis and *P. nebulosus* were less armoured than the melanistic species found in the other clades, due to the absence of certain spines (Table 1). Both species lacked spines on the posterior margin of the head, whereas both populations of *P. capensis* also had no spines on the trunk and neck. Individuals from the northern and southern populations of *P. capensis* did not differ significantly from each other in any of the spine lengths (Tail: $P = 0.996$; hind leg: $P = 1.00$; front leg: $P = 0.085$; and tympanum: $P = 0.21$), but when we excluded *P. nebulosus* from the analysis, there was a significant difference in spine length on the hind limb, with individuals from the northern population having slightly longer spines than those of the southern population ($t = 3.36$, df = 30, $P < 0.05$). Individuals from both northern and southern populations of *P. capensis* had significantly longer spines on the tympanum than those of *P. nebulosus* ($F = 22.31$; df = 41; $P < 0.05$ for both cases), but did not differ from *P. nebulosus* in terms of the length of the spines of the tail ($P = 0.581$ and $P = 0.622$, respectively), hind leg ($P = 0.592$ and $P = 0.603$, respectively) and front leg ($P = 0.813$ and $P = 0.589$, respectively).

5.3.2 Osteoderm development

The osteoderm index obtained for each species is summarized in Table 2. Histological sections show that in the majority of species investigated here, osteoderms were always present, well-developed and covering the breadth or almost the breadth of the scale. The osteoderms articulated closely with one another and perforations were sometimes present within the bone (Fig. 1-2). In areas where the adjacent scales overlapped, two layers of osteoderms were often observed. Within-clade comparisons revealed that the two melanistic species in the *cordylus-niger-oelofseni* clade displayed no difference in terms of osteoderm development/thickness ($P = 0.229$) (Fig. 1). There was, however a significant difference between *C. oelofseni* and *C.*

Table 2. Osteoderm indices for melanistic cordylid species and their closest relatives. Melanistic species are indicated by *.

Species	***N***	**Osteoderm index ± SD**
Cordylus cordylus	6	36.4 ± 7.1
*Cordylus oelofseni**	5	26.4 ± 3.7
*Cordylus niger**	6	30.3 ± 3.1
Cordylus polyzonus	6	42.4 ± 6.0
*Cordylus polyzonus**	6	35.3 ± 4.9
Cordylus lawrenci	1	46.0
*Cordylus peersi**	1	57.6
*Pseudocordylus nebulosus**	3	1.65 ± 0.24
Pseudocordylus capensis (north)*	1	3.42
Pseudocordylus capensis (south)*	6	4.63 ± 1.88

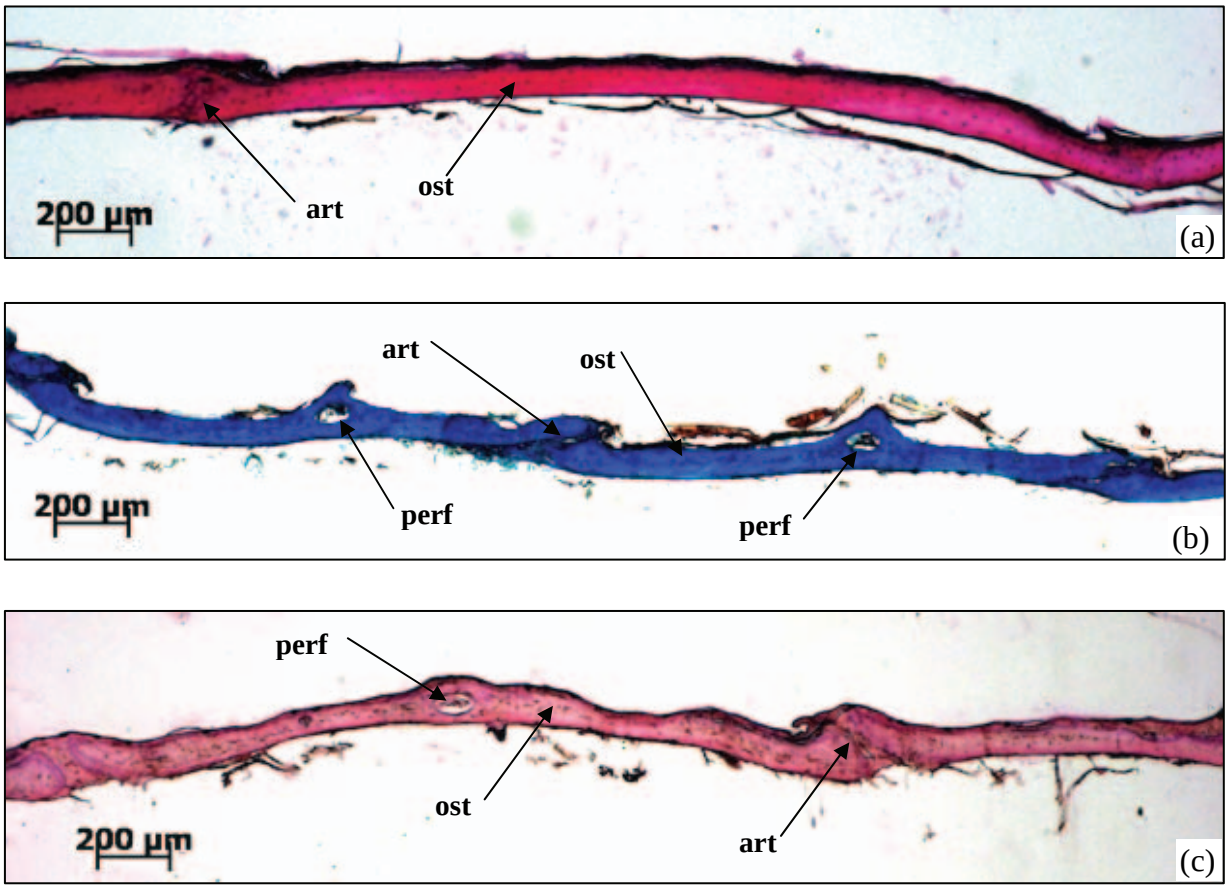

Figure 1. Serial histological sections of dorsal skin showing the well-developed osteoderms of *Cordylus niger* (a), *Cordylus oelofseni* (b) and *Cordylus cordylus* (c). art = articulation; ost = osteoderm; perf = perforation.

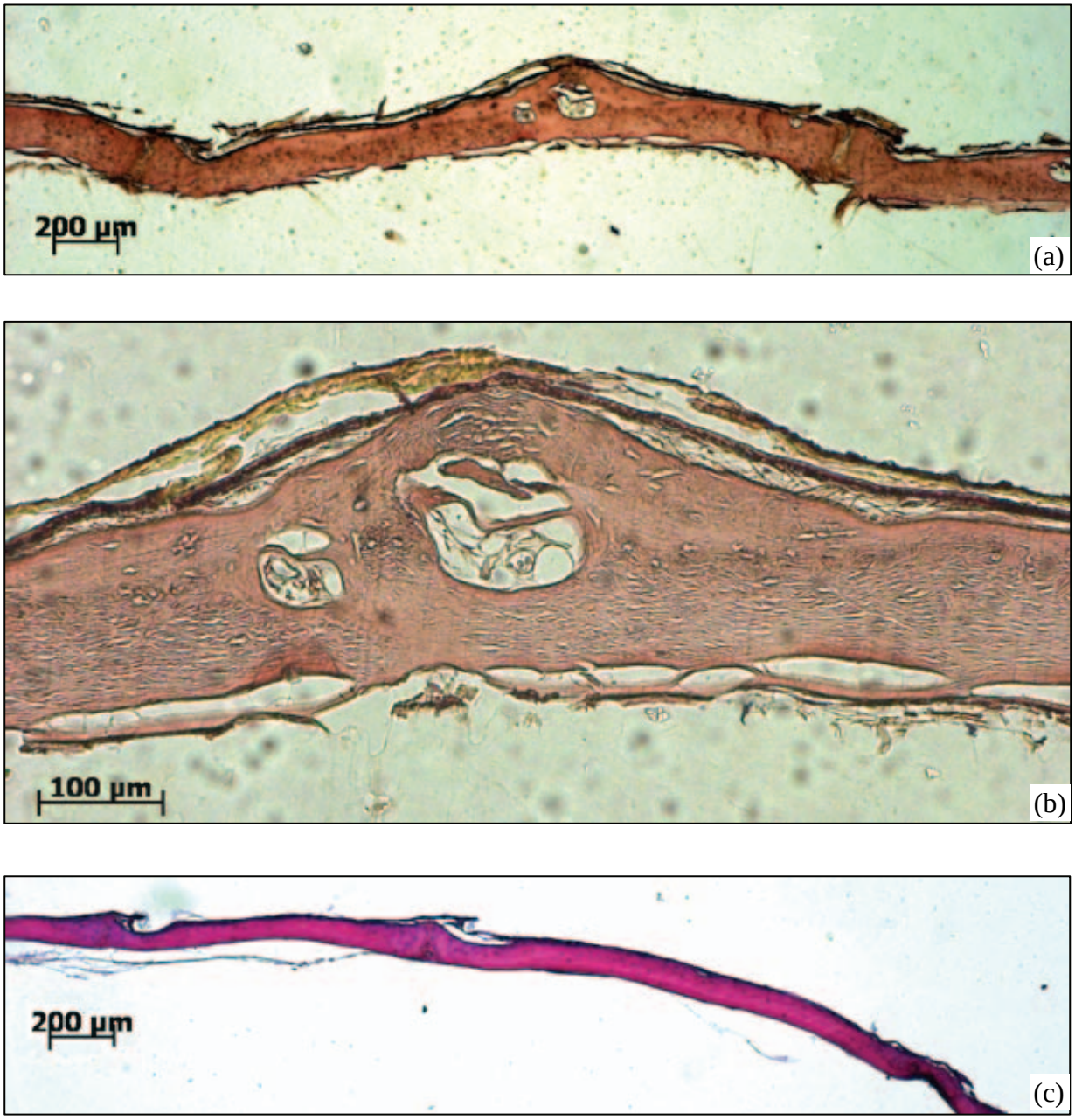

Figure 2. Serial histological sections of dorsal skin for *Cordylus peersi* (a and b) and *Cordylus lawrenci* (c).

cordylus ($P < 0.05$), with the non-melanistic species having better developed/thicker osteoderms than the melanistic species. There was only a slightly non-significant difference between *C. niger* and *C. cordylus* ($P = 0.055$). Non-melanistic *C. polyzonus* also had significantly better developed/thicker osteoderms than melanistic *C. polyzonus* ($P < 0.05$). From Figure 2 it is evident that *Cordylus peersi* had better developed/thicker osteoderms than *C. lawrenci*.

In *Pseudocordylus capensis* and *P. nebulosus*, the osteoderms were much smaller and thinner than in the other species and did not articulate with one another, but were rather present as isolated dermal ossifications (Fig. 3-4). Osteoderms were present in all members of the southern population of *P. capensis*, but in the northern population, it was absent in all but one individual where only remnants were visible. This individual also had the largest SVL of the northern population specimens.

5.3.3 Degree of body armour in melanistic cordylids

From the PCA it was evident that melanistic cordylids differed in their degree of body armour (Fig. 5). *Cordylus peersi* was the most spinose and had well-developed/thick osteoderms, whereas the northern and southern populations of *Pseudocordylus capensis*, as well as *P. nebulosus* had lesser developed/thinner osteoderms and were the least spinose. As mentioned previously, *P. capensis* completely lacked spines on the trunk and neck, as well as the posterior margin of the head (Table 1).

5.3.4 Escape behaviour in melanistic cordylids

The melanistic species displayed significant differences in the distances they were observed from the crevice and the distance they ran before entering a refuge (F-value: 12.13, $P < 0.001$,

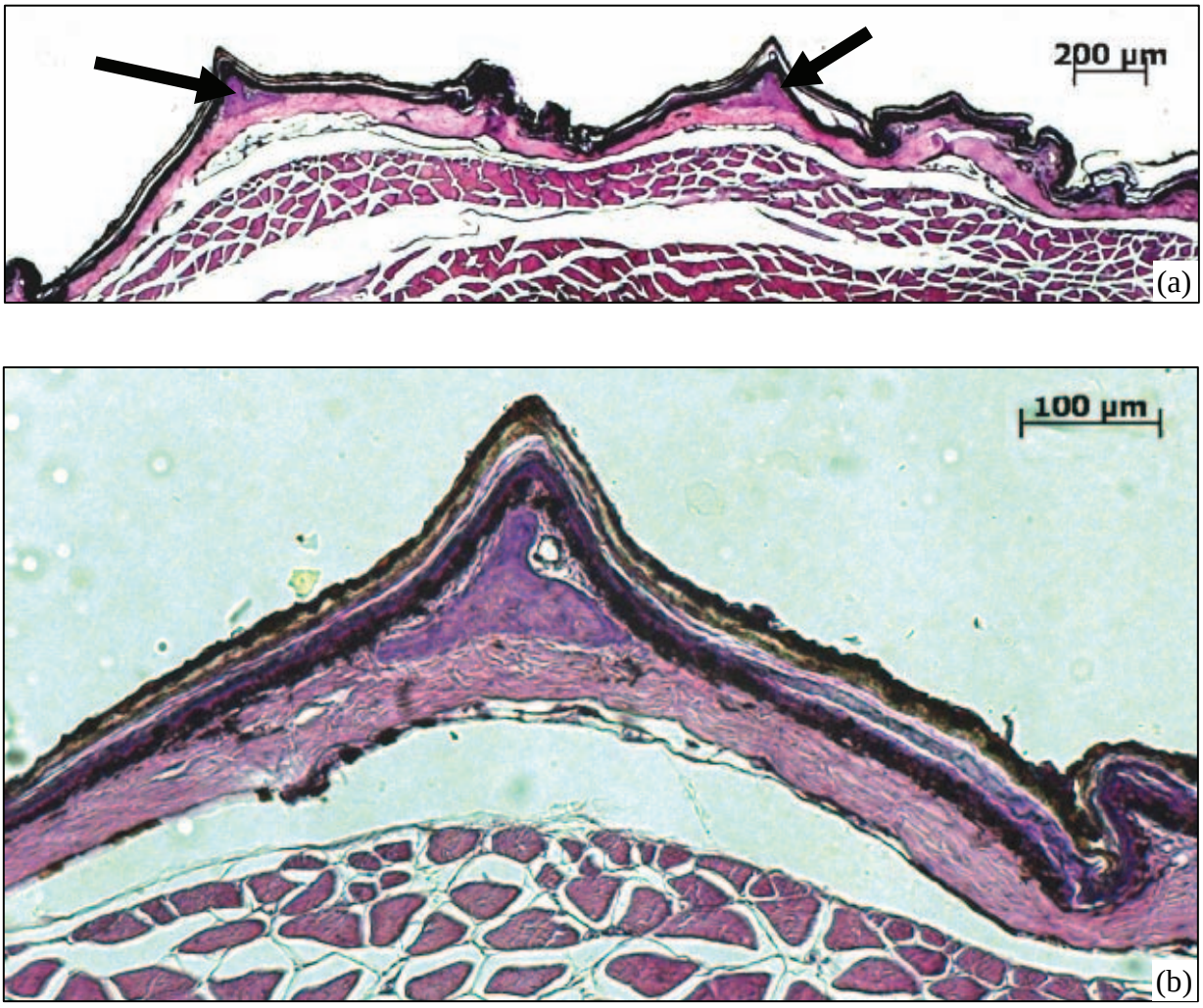

Figure 3. Serial histological sections of dorsal skin for *Pseudocordylus nebulosus*. (a) depicts the isolated nature of the osteoderms (indicated by the arrows) and (b) shows a close-up of an osteoderm.

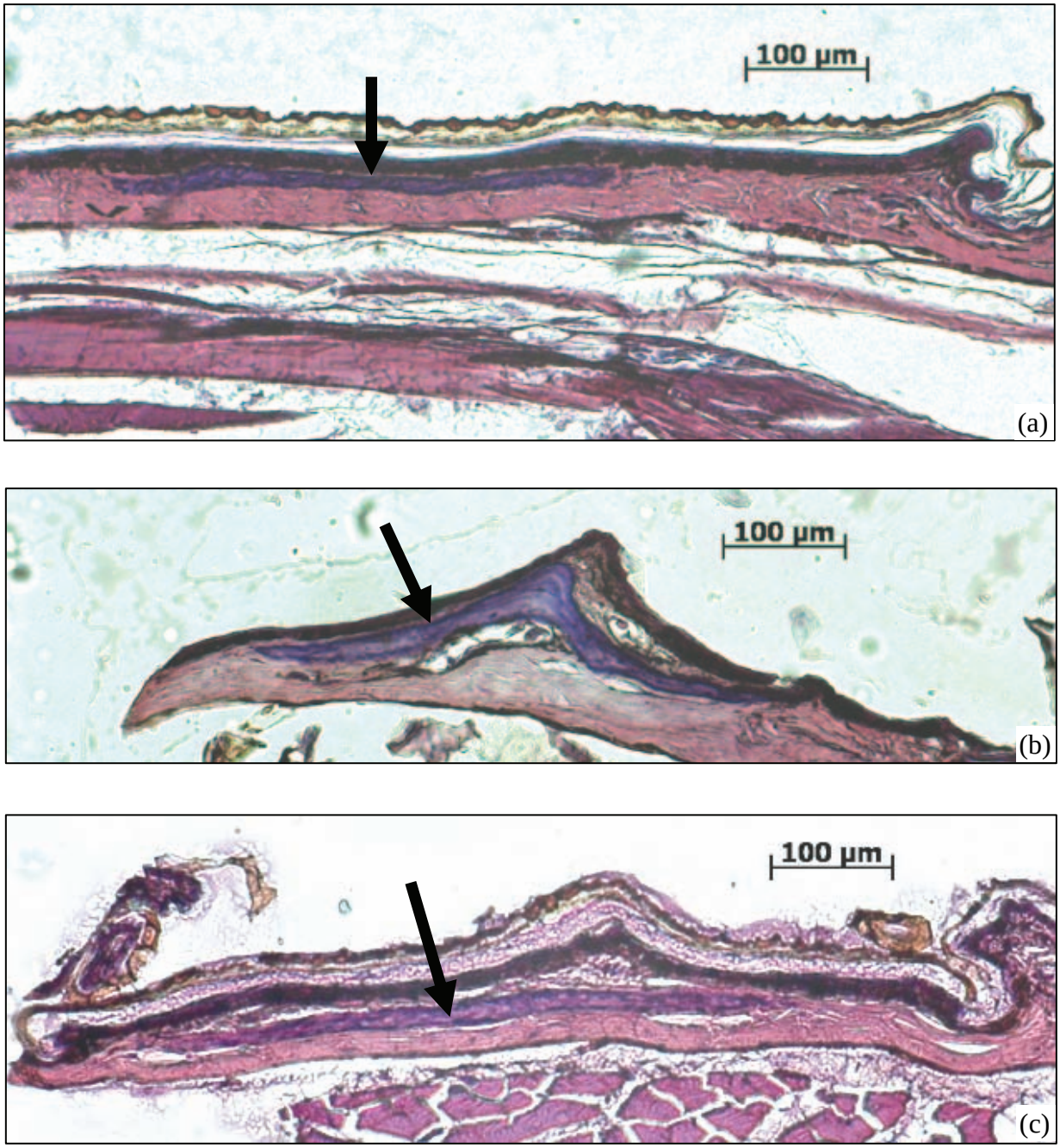

Figure 4. Serial histological sections of dorsal skin for *Pseudocordylus capensis*. Remnants of osteoderms were visible in a single individual from the northern population (a), while osteoderms were present in all individuals from the southern populations (b and c). Osteoderms are indicated by arrows.

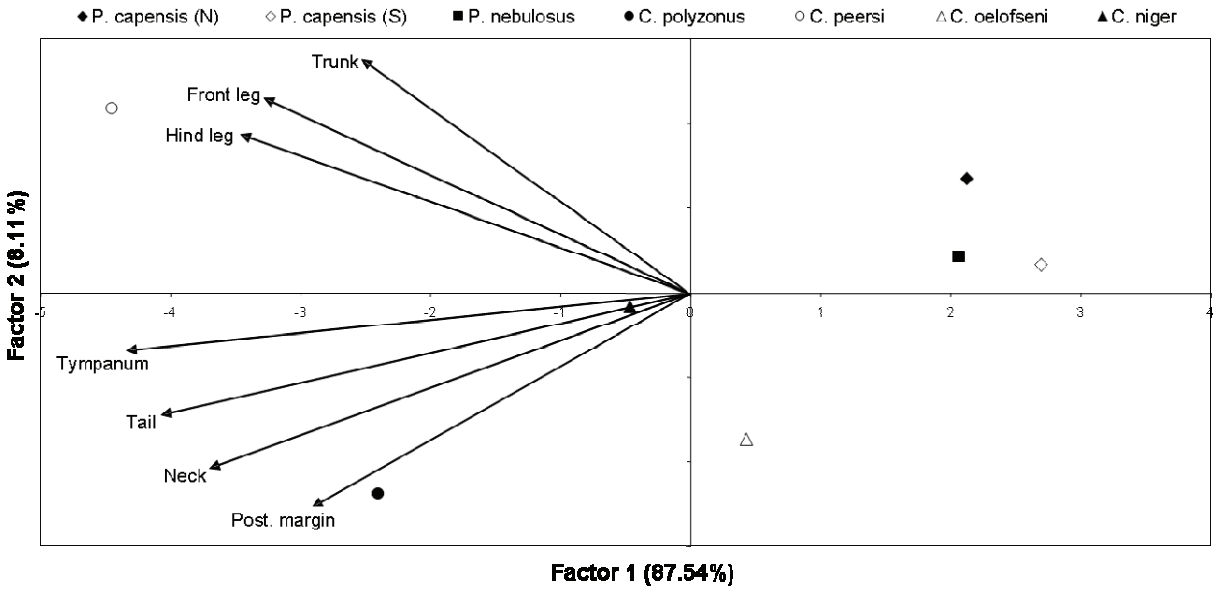

Figure 5. PCA results on size-adjusted body armature data for melanistic cordylids.

Table 3. Summary of average distances ± SE moved by melanistic cordylids.

Species	***N***	**Avg. distance from crevice (cm)**	**Avg distance moved before entering refuge (cm)**
P. capensis	44	107.07 ± 12.77	156.93 ± 18.85
P. nebulosus	45	65.08 ± 8.05	102.47 ± 11.50
C. polyzonus	38	48.95 ± 6.04	50.54 ± 6.18
C. oelofseni	73	30.59 ± 3.76	50.38 ± 7.77
C. niger	26	39.04 ± 5.02	44.20 ± 5.54

Table 3). *Pseudocordylus capensis* were found significantly further away from the crevice than all the other species ($P < 0.05$ for all cases). The only other significant difference was that *C. niger* and *C. oelofseni* were found to be closer to their crevices than *P. nebulosus* ($P < 0.001$ for both cases). When lizards were approached, *P. capensis* ran significantly longer distances before entering a refuge than any of the other species ($P < 0.05$ for all cases). The majority of lizards immediately retreated to the nearest crevice when approached by an observer, thus only moving the distance from where they were first observed to the crevice. In contrast, *P. capensis* seldom retreated immediately, but rather moved away from the observer. Twenty five percent of *P. capensis* individuals ran more at least 2.0 m, and 11 % ran at least 3.0 m before entering a refuge. In contrast, the rest of the species seldom moved more than 1.0 m away from their crevices.

5.4 DISCUSSION

In this study I found that in the *cordylus-niger-oelofseni* and *polyzonus* clades, melanistic species/populations were less spinose and had lesser developed osteoderms than non-melanistic ones. This is in accordance with my prediction that during the evolution of melanism in cold environments, lizards would have spent more time basking and would have been more exposed to aerial predation. As speed and crypsis are efficient anti-predatory mechanisms under these circumstances, one would expect a reduction in armour to expedite greater running speed and agility.

Presently, melanistic members in the two clades are restricted to areas along the coast where there is a high incidence of fog, and along the Cape Fold Mountains where there is a high incidence of orographic fog and cloud cover (Janse van Rensburg *et al*. 2009; Chapter 2). It is expected that melanism will be advantageous under these conditions of limited solar

radiation in increasing the rate of adsorption of solar radiation (Clusella-Trullas *et al*. 2007a). It is also expected that extended basking times will be required under these conditions (see e.g. Van Damme *et al*. 1990). Not only will extended basking times result in increased exposure to aerial predation, but a melanistic body colour may also not be optimal in terms of crypsis, increasing exposure to aerial predation even further. When basking on suitable perches some distance away from their shelters, melanistic lizards will need to be fast to reach the safety of their crevices in the event of an aerial attack. Degree of armour and running speed are negatively correlated (Losos *et al*. 2002) and one would therefore expect a reduction in armour in melanistic populations occurring in environments where solar radiation levels are low.

In the *peersi-lawrenci* and *nebulosus-capensis* clades we observed opposite patterns. *Cordylus peersi*, jet-black in colour, is a distinctly spinose lizard, also having thick osteodermal plates. In fact, it is by far the most spinose of the melanistic cordylids and even more spinose than most non-melanistic cordylids. If I am correct in my assumption that degree of body armour will be a reflection of the relative importance of aerial versus terrestrial predation, the heavy armour of *C. peersi* should be an indication of limited exposure to aerial predation, terrestrial predation dictating its morphology. Why would this be? Unlike other melanistic cordylids, *C. peersi* occurs in a relatively warm environment (Janse van Rensburg *et al*. 2009) where melanism may be a constraint (Clusella-Trullas *et al*. 2007a; Janse van Rensburg *et al*. 2009; Chapter 2). It is therefore to be expected that *C. peersi* will spend less time basking in the open and more time in shady areas. It will consequently be less exposed to aerial predation, with the resultant increase in the influence of terrestrial predation on morphology, i.e. an increase in the degree of body armature.

If the above scenario were to be true, one would have expected only a minor increase in body armature relative to that of melanistic cordylids occurring in cool environments. The

high degree of spinosity and thick osteoderms displayed by *C. peersi* is a clear indication that other factors may also be at play, influencing degree of body armature. *Cordylus peersi* is one of two group-living rock-dwelling cordylid species occurring along the West Coast of South Africa (Fell 2005). The other one, *C. cataphractus*, heavily relies on termites as a food source and sources termites at the foraging ports of the termite nests (Effenberger 2004). Harvesting termites away from the crevice at the termite foraging ports and predation pressure by terrestrial predators associated with these foraging excursions is seen as the primary driving force in the evolution of heavy armour and the tail-biting anti-predatory behaviour displayed by *C. cataphractus* (Mouton *et al.* 2000, 2005; Effenberger 2004). The heavy armour, however, seriously compromises agility in this species (Losos *et al*. 2002), and it is therefore more prone to aerial predation during general maintenance behaviour at the rock shelter than other cordylids lacking armour would be (Mouton & Flemming 2001; Losos *et al*. 2002). Hayward (2008) established that the impact of aerial predation is offset by living in groups, individuals in groups benefiting from increased vigilance associated with group-living. There is thus a distinct possibility that the heavy armour of *C. peersi*, like in the case of *C. catapractus*, reflects foraging under vegetation cover at distances too far away from rock crevices for speed to be an effective means of escape from terrestrial predators.

In the *nebulosus-capensis* clade, degree of armour was lowest in the northern populations of *P. capensis*, occurring in relatively warm environments. While all individuals of *P. nebulosus* and *P. capensis* from Landdroskop in the south had osteoderms, only one very large (old?) individual in the sample from the northern population investigated had remnants of osteodermal plates. This ties in with earlier observations that *P. capensis* has more granular body scalation the northern, warmer part of its distribution range than in the southern, cooler parts (Herselman, Mouton & Van Wyk 1992). Based on my assumption that the relative

intensity of aerial versus terrestrial predation will determine degree of body armour in rock-dwelling cordylids, as well as my results on armour in the *cordylus-niger-oelofseni* and *polyzonus* clades, I would have predicted that the northern populations of *P. capensis*, occurring in warmer environments, would have shown a greater degree of armature than the southern populations occurring in cool environments. I would have guessed that *P. capensis* individuals would spend less time basking in warm environments, that exposure to aerial predation would be lower than in cool environments, and consequently that selection for speed will be suppressed, resulting in a greater degree of armour developing.

The deviation of the northern *P. capensis* populations from the expected pattern is probably not difficult to explain. The fact of the matter is that *P. capensis* retained its melanistic body colour in these warm northern environments. It has already been established that *P. capensis* frequents large boulders and vertical rock faces in these warm northern areas (Chapter 3) and it was concluded that those melanistic cordylids that are presently not restricted to cool environments are able to survive in warm environments by using large rock formations with their associated wider range of thermal opportunities. Living on large bare rock surfaces will, however, increase visibility to aerial predators and selection for speed should override selection for armour. The reduction in osteoderms (this study) and the granular scaling found in the northern populations (Herselman *et al*. 1992) underscore the earlier observation that northern populations frequent bare rock surfaces. *Platysaurus broadleyi*, another cordylid frequenting bare rock surfaces (Branch & Whiting 1997; Chapter 6), also lacks osteoderms, has granular scaling (Branch & Whiting 1997) and is extremely fast (Branch 1998; Losos *et al*. 2002).

Janse van Rensburg *et al*. (2009) found that both *P. capensis* and *C. peersi* occur in relatively warmer environments than other melanistic cordylids. Both should thus have to deal

with the constraints of melanism in warm environments. Although both species frequents large boulders (Chapter 3), *Cordylus peersi*, as the heavy armour indicates, apparently stays close to the crevice at all times (Losos *et al.* 2002; own observations). *Pseudocordylus capensis* individuals, on the other hand, have relatively large home ranges (Chapter 6). Why did these two melanistic cordylids evolve apparently different strategies to overcome possible constraints of melanism in warm environments? How can *C. peersi* individuals survive by staying close to their crevices at all times given that activity time will be severely restricted by limited thermal opportunities close to the crevice? The most obvious explanation for this anomaly is the different phylogenetic histories of the two species. *Pseudocordylus capensis* belongs to a clade of species which all show high agility, a low degree of armour and a less sedentary foraging strategy (Frost *et al.* 2001; Losos *et al*. 2002; Chapter 6). Members of the *Cordylus* clade to which *C. peersi* belongs, are all strict sit-and-wait foragers, have well developed armour and are less agile than members of the above clade (Mouton & Van Wyk 1997; Frost *et al*. 2001; Losos *et al*. 2002). The option of increasing home range size to include a wider spectrum of thermal opportunities, because of phylogenetic constraints, may thus not have been available to *C. peersi*. It has been suggested that *C. peersi*, because of its jet black colour, needs special microhabitats to overcome the constraints of melanism and that these are provided by the thin flakes on the large granite boulders which they frequent. These special shelters are in short supply and the lizards are forced to share shelters, therefore the grouping behaviour displayed by the species. In these small aggregations of strict sit-and-wait foragers, competition for food will, however, be high, necessitating the regular use of an additional food source. In *C. cataphractus*, termitophagy, allows individuals to live in groups. During activity individuals will stay within centimetres of the safety of their crevice (Visagie 2001), but from time to time, making use of vegetation cover, will visit foraging ports of

termite nests when the termites are active (Effenberger 2004). Within a short period of time they can gorge themselves with food and return to the safety of the crevice. These excursions in *C. cataphractus* resulted in the evolution of heavy armour as aerial predation is minimised by the use of vegetation cover (Effenberger 2004). It is clear that detailed studies of thermoregulation and foraging in *C. peersi* are first required before more definite explanations for the unexpected armoured morphology of *C. peersi* can be provided.

Another aspect that needs to be investigated is the physical properties of the rock types *P. capensis* and *C. peersi* are using. *Cordylus peersi* is found on the large Namaqua basement gneisses, whereas *P. capensis* is found on the Gifberg quartzites of the Cape Supergroup. Both are metamorphic rocks, but have different physical properties. Quartz content can influence thermal conductivity (i.e. the ability to conduct heat) in rocks. In general, quartzite has a high quartz content and high thermal conductivity, whereas gneiss has a low quartz content and low thermal conductivity (Clauser & Huenges 1995). Because of its low thermal conductivity gneiss is usually cool to the touch, unlike quartzite that will heat up rapidly during the day (pers. obs.). Gneiss and quartzite also differ in terms of their joint patterns. When gneiss weathers it forms sheet joints parallel to the surface and erodes in concentric layers (almost like an onion) to form exfoliation domes (Thornbury 1969). Quartzite, on the other hand, is very resistant to weathering and often forms ridges. These formations can have networks of deeper-reaching horizontal and vertical cracks.

In conclusion, melanistic members of the *cordylus-niger-oelofseni* and *polyzonus* clades are less armoured than their closest non-melanistic relatives, supporting the hypothesis that in cold environments melanistic cordylids bask more and are accordingly more exposed to avian predators than their non-melanistic relatives. The two melanistic species of which populations also occur in warm environments, *C. peersi* and *P. capensis*, displayed opposite patterns, a

distinct reduction in armour in northern populations of *P. capensis* and an expansion of armour in the case of *C. peersi*. The reduction in the case of *P. capensis* can be explained in terms of greater visibility to aerial predators due to the use of large bare rock surfaces. In the case of *C. peersi*, the heavy armour cannot be explained with the information at hand and further study is needed.

CHAPTER 6

FORAGING BEHAVIOUR AND SPACE USE IN THE GRACEFUL CRAG LIZARD, *PSEUDOCORDYLUS CAPENSIS*: LIFE ON LARGE ROCK SURFACES*

6.1 INTRODUCTION

Given that foraging success ultimately affects reproductive success, foraging behaviour is considered one of the fundamental attributes of any animal (Travers & Sih 1991; Miles *et al*. 2007). Foraging behaviour has accordingly been an important topic in studies of the ecology and evolutionary biology of lizards (Perry & Pianka 1997; Perry 2007). Based on empirical data on distances moved, proportion of time moving (PTM) and moves per minute (MPM), species have been classified as either ambush or widely foraging predators (Pianka 1966; Huey & Pianka 1981; Cooper *et al*. 1999). This division has, however, been shown to be artificial and today most authors consider these two modes as extremes on a continuum (Perry 1999, 2007).

Based on low MPM and PTM values recorded for species investigated to date, the African family Cordylidae has been described as a clade of classical ambush foragers (Cooper, Whiting & Van Wyk 1997; Mouton & Van Wyk 1997; Whiting 2007). Mouton & Van Wyk (1997) proposed that the correlated shifts from widely foraging to ambush foraging, and from a ground-dwelling lifestyle to a rock-dwelling one in the immediate ancestor of the Cordylidae was brought about by cooler climates. At least two cordylid species have, however, been found to display distinctly greater movement rates during activity than other cordylids. PTM-values of 6-7% and MPM-values of 0.5-1.2 have been recorded for *Platysaurus broadleyi* and *Pseudocordylus capensis*, whereas in other cordylids PTM is typically below 3% and MPM below 0.4 (Cooper *et al*. 1997; Whiting

*Janse van Rensburg, D.A. & Mouton, P.le F.N. 2009. Foraging behaviour and space use in the Graceful Crag Lizard, *Pseudocordylus capensis*: life on large rock surfaces. *African Journal of Herpetology* **58**: (in press).

2007). Lizard foraging mode is generally remarkably stable within entire clades of lizards (Cooper 1994, 1995) and deviations from the normal pattern within clades, should thus be highly informative with regard to the factors allowing an organism to alter its foraging behaviour (Whiting 2007). Greeff & Whiting (2000), for example, demonstrated that *P. broadleyi* exhibits flexible foraging behaviour by ambushing insects and by actively searching for fruit.

Whereas foraging behaviour is now well-studied in *P. broadleyi*, few data are available for *P. capensis*. This species offers an additional opportunity to investigate factors responsible for deviations from the typical strict ambush foraging strategy followed by most cordylids. *Pseudocordylus capensis* is one of several melanistic cordylids found in the Western and Northern Cape Provinces of South Africa (FitzSimons 1943; Mouton & Oelofsen 1988; Mouton & Van Wyk 1995). Whereas the majority of melanistic cordylids have restricted distributions in cool coastal or montane localities (Badenhorst 1990; Janse van Rensburg, Mouton & Van Niekerk 2009; Chapter 2), *P. capensis* has a wide distribution, occurring from cool montane areas to warm lowland areas (Janse van Rensburg *et al*. 2009; Chapter 2). In warm areas, *P. capensis* is exclusively associated with large boulders or cliff faces (Chapter 3). While the morphology of most melanistic cordylids excludes them from using large rock formations, the long limbs and lack of armour of *P. capensis* allow this species to scale large boulders and cliff faces (Losos *et al*. 2002; Chapter 3). Large rock formations provide a wide range of microclimates, which probably allows this species to be successful even in warm environments (Chapter 4). At the same time, large, barren rock surfaces may have low food availability, necessitating changes in foraging behaviour.

Species that vary in foraging mode exhibit consistent differences in space use (Stamps 1977). Ambush foragers usually stay close to the safety of the crevice and heavily

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rely on vision to find prey. An ambush foraging strategy, combined with high visual orientation, is advantageous for successful home range defence, as a lizard would be able to forage and watch out for intruders simultaneously (Stamps 1977). Widely foraging foragers have to search for prey by means of visual and chemical stimuli and they normally have to cover large areas during their searches. The habitats these lizards forage in also often have poor visibility, making it difficult to detect intruders from large distances (Stamps 1977). The objective of my study was to verify the high PTM and MPM values recorded for *P. capensis* by Cooper *et al*. (1997). In addition, I recorded baseline data on home range size and spacing patterns of male and female *P. capensis.* Because of the expected low food availability on large rock surfaces, I predicted that both males and females will have relatively large home ranges. Due to the difficulty of defending a large home range (Stamps 1977), I expected considerable overlap in the home ranges of individuals and low levels of aggression among individuals compared to other cordylids.

6.2 Materials and Methods

6.2.1 Study sites

Foraging data for *P. capensis* were collected at three localities in the Western Cape Province, South Africa. Two localities are in the northern section of the species' distribution range, namely the Gifberg Holiday Farm in the Gifberg Mountains (31°48.567'S, 18°47.583'E) and the Stadsaal Caves in the Matjiesrivier Nature Reserve (32°31.353'S, 19°19.029'E). The third locality, Landdroskop (34°02.800'S, 18°59.633"E), is in the southern part of the species' range (Janse van Rensburg *et al*. 2009). Spacing patterns in *P. capensis* were investigated at the Gifberg Holiday Farm. A ravine with a seasonal waterfall was selected as study site, as this locality provided a simple set-up

where several individuals could be observed simultaneously by only two to three observers.

The two northern localities occur in a semi-arid winter rainfall region, characterized by a dry summer with high maximum temperatures (Low & Rebelo 1996; MacKellar *et al.* 2007). Average summer temperature is 25°C (Truter 1998), but temperatures higher than 40°C have been recorded, even in winter (Cowling, Esler & Rundel 1999). Rainfall ranges from 50-400 mm, with an average of 150 mm per year (Truter 1998; Cowling *et al*. 1999). The Landdroskop locality is in the Hottentots Holland Mountains, at an altitude of 1000-1500 m. The area mainly receives winter rain with the mean annual rainfall being of the highest in South Africa, exceeding 1200 mm per year (Dent *et al*. 1989). Sirgel (1985) reported that this area experiences overcast conditions for at least 200 days per year. Average summer temperature for this locality is in the region of 19°C (Janse van Rensburg *et al*. 2009).

6.2.2 Foraging behaviour

Data on foraging behaviour were collected during October 2008 (spring) at the Gifberg locality, during February 2009 (late summer) at the Stadsaal Caves, and during September 2005 (spring) and May 2009 (autumn) at the Landdroskop locality. Two criteria were used to infer foraging behaviour: 1) the number and duration of movements related to foraging, quantified as the movements per minute (MPM) and the proportion of time spent moving (PTM); and 2) foraging speed, quantified as average speed (AS) and speed while moving (MS) (Cooper & Whiting 1999; Cooper *et al*. 2005).

Field observations of foraging behaviour in *P. capensis* were conducted on sunny days when lizards were active. An observer located a lizard with binoculars or unaided vision while walking slowly through an area. Binoculars were used to observe a specific

individual for 10 consecutive minutes, or until the lizard moved out of view, but always for at least a minimum of 1.5 minutes. To ensure that individuals were only observed once, each area was only sampled once. Time spent moving, time stationary, and distances moved were recorded for each individual. Only translational movements were recorded. Several foraging variables were calculated from the movement data: MPM; PTM; AS (total distance moved divided by total observation time in seconds); and MS (total distance divided by time moving). Data were compared by means of Mann-Whitney *U*-tests.

6.2.3 Relative home range size, overlap and social behaviour

Data on spacing patterns and behaviour were collected during February 2008. For easy identification from a distance, sixteen adult lizards (nine females and seven males) were individually marked on the sides of the head and on the tail with non-toxic Dala acrylic paint (www.dala.co.za) which conforms to the ASTM D4236 standard. *Pseudocordylus capensis* is an inquisitive species and not easily frightened by human interference (pers. obs.), and the hiking trail leading through the ravine has resulted in this particular population becoming habituated to human presence. It was thus possible to observe the lizards with binoculars or unaided vision from a relatively close (3 – 10 m) distance without any disturbance. The three observers were also positioned in such a way that the whole ravine could be observed with minimal amount of moving around. Observations commenced at 07:30 each morning and ended around 18:00 when the majority of lizards became inactive. The area was continuously scanned for lizard activity. When a lizard was spotted for the first time, its position was recorded on a photograph of the area. If a lizard was moving, I recorded the position of each stop on the photograph.

Because of the complexity of the terrain, including both horizontal and vertical surfaces and many interconnecting crevices not accessible to the observers, it was virtually

impossible to determine actual home range size for the marked individuals. Instead, because all the individuals observed occurred along the vertical sides of the ravine, I measured space use in the vertical plane only (hereafter referred to as vertical area of space use) as a substitute for home range. For each individual's area of space use, the horizontal dimension was taken as the horizontal distance between the two location points furthest away and the vertical dimension as the vertical distance between two location points furthest away. Vertical area of space use was calculated using the formula for the area of an ellipse: ½ abπ, where a and b are the recorded horizontal and vertical distances. For each of the marked individuals, I also determined mean daily total distance moved over the four day period.

Mann-Whitney *U*-tests were used to determine if there were any differences in the recorded vertical areas of space use and mean daily total distances moved by males and females during the summer season. I also counted the number of males and females whose space use overlapped with that of other males and females. When an interaction between two or more individuals was observed, I noted the duration and recorded the behaviour of the individuals involved.

6.3 RESULTS

6.3.1 Foraging behaviour

MPM and PTM: At least 50% of the total number of observations of *P. capensis* (*n* = 76) lasted the set maximum of 10 minutes. MPM and PTM recorded for *P. capensis* at all three localities and during all times of the year were consistently higher than those recorded for other cordylid species, with the exception of *Pseudocordylus broadleyi* (Table 1). The values that we recorded for *P. capensis* were in the same range as those recorded for this species by Cooper *et al*. (1997) at Papkuilsfontein in the northern section of the species'

range (Table 1) during March. No consistent seasonal pattern in movement rates was observed. At Landdroskop, significantly lower PTM values were recorded during September than during May (T = 303.0, P < 0.05). The difference in mean MPM for the two months were only slightly non-significant (T = 272.0, P = 0.057). Exceptionally high values were recorded during September at the Gifberg locality, significantly higher than the values recorded at Landdroskop during September (MPM: T = 225.5, P < 0.05; PTM: T = 232.5, P < 0.05). Values recorded during February, March and May at the Stadsaal Caves, Papkuilsfontein (Cooper *et al*. 1997) and Landdroskop, respectively, were of a similar range (Table 1). Variation among individuals was consistently high at all localities. Preliminary observations of *P. nebulosus*, occurring sympatrically with *P. capensis* at Landdroskop, yielded PTM and MPM-values of the same magnitude as those recorded for *P. capensis* (Table 1).

Several feeding attempts were recorded during the observation of *P. capensis*: Landdroskop: September: N = 13; May: N = 11; Gifberg: N = 8; and Stadsaal Cave: N = 10. I also noted that *P. capensis* tongue-flicked regularly when stationary as well as when moving. At the Stadsaal Caves site, *P. capensis* was observed to eat the fruit of the Klipkershout Tree (*Maytenus oleoides*), and at Landdroskop, the fruit of the Dune Crowberry (*Rhus crenata*).

AS and MS: *Pseudocordylus capensis* displayed varying values for AS and MS (Gifberg (N = 12): AS: 0.012 ± 0.006; MS: 0.100 ± 0.024; Landdroskop (dry season, N = 14): AS: 0.006 ± 0.001; MS: 0.078 ± 0.012; and Landdroskop (wet season, N = 17): AS: 0.002 ±

Table 1. Summary of recorded movements per minute (MPM) and percentage time spent moving (PTM) values for several species of Cordylidae. Data were compiled from 1) Cooper *et al*. (1997); 2) Du Toit *et al*. (2002); 3) Mouton *et al*. (2000), and 4) this study.

Species	**MPM**		**PTM (%)**			**Obs. time**
(Data source)	***x* ± S.E.**	**Range**	***x* ± S.E.**	**Range**	***n***	**(min)**
Platysaurus capensis (1)	1.27 ± 0.32	0.0 - 6.82	6.62 ± 1.58	0.0 - 2.17	22	205.4
Pseudocordylus capensis (Landdroskop, dry season, 4)	1.13 ± 0.17	0.2 - 2.27	8.52 ± 1.53	1.83 - 16.81	14	87.4
P. capensis (Stadsaal Cave, Cederberg area, dry season, 4)	0.78 ± 0.15	0.0 - 3.31	6.56 ± 1.42	0.0 - 25.35	33	257.3
Pseudocordylus capensis (Gifberg, after rainy season, 4)	1.69 ± 0.39	0.10 - 3.78	11.59 ± 3.81	0.33 - 45.90	12	73.78
P. capensis (Landdroskop, after rainy season 4)	0.78 ± 0.12	0.10 - 2.67	3.30 ± 1.03	0.17 - 15.56	17	127.0
P. capensis (previous study, 1)	0.59 ± 0.20	0.0 - 1.11	6.77 ± 2.0	0.0 - 14.06	6	51.9
P. microlepidotus (1)	0.0 ± 0.0	-	0.0 ± 0.0	-	7	70.0
P. nebulosus	0.81 ± 0.17	0.0 - 2.50	4.28 ± 0.98	0.0 - 11.25	16	97.5
Chamaesaura anguina (2)	0.37 ± 0.21	0.0 - 0.70	1.92 ± 0.93	0.0 - 3.50	12	n.a
Cordylus cataphractus (3)	0.23 ± 0.08	0.0 - 0.96	2.20 ± 0.71	0.0 - 7.19	15	121.1
C. cordylus (1)	0.09 ± 0.02	0.0 - 0.70	0.27 ± 0.08	0.0 - 2.50	45	427.83
C. imkeae (1)	0.0	-	0.0	-	1	10.0
C. niger (1)	0.09 ± 0.03	0.0 - 0.60	0.19 ± 0.06	0.0 - 1.33	36	350.38
C. polyzonus (1)	0.04 ± 0.02	0.0 - 0.34	0.15 ± 0.07	0.0 - 1.00	17	157.23

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0.001; MS: 0.053 ± 0.008). Values for *P. nebulosus* were similar to the values recorded for *P. capensis* at Landdroskop (AS: 0.003 ± 0.001; MS: 0.058 ± 0.010).

6.3.2 Relative space use size

Both male (21.71 ± 20.04 m) and female *P. capensis* (25.96 ± 28.44 m) travelled substantial distances on a daily basis, with no significant difference between the sexes (Mann-Whitney *U*-test: $U = 128.00$, $Z = 0.182$, $P = 0.855$). Individuals moved considerably longer distances along the horizontal than the vertical axis (males: 19.00 ± 18.74 m horizontal, 3.16 ± 1.82 m vertical; females: 22.89 ± 26.84 m horizontal, 3.27 ± 2.30 m vertical). Both males (215.12 ± 253.51 m^2) and females (218.75 ± 233.18 m^2) had relatively large vertical areas of space use, with no significant differences between the sexes (*t*-test: $t = 0.734$, $df = 12$, $P = 0.477$).

Pseudocordylus capensis does not seem to display specific site fidelity as several individuals were observed in different shelters each morning.

6.3.3 Space use overlap

Areas of space use of males often overlapped completely with those of one to five females (Fig. 1). Space use of all individual males overlapped with that of at least one female, sometimes with those of up to five females. Space use areas of individual males also overlapped with those of other males (range: 0-3), but the degree of overlap was limited and restricted to the periphery. Space use areas of individual females overlapped with those of up to four males and up to three females. Only six encounters were recorded during the four-day observation period, and of these only three were aggressive, one between two males, one between two females and one between two unmarked individuals (Fig. 2).

Figure 1**.** Spacing patterns of male and female *Pseudocordylus capensis* at Gifberg Holiday Farm. The northern (a) and southern (b) slopes of the ravine are shown here. Relative space use areas are indicated by shaded areas (males) and dashed lines (females).

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Figure 2. Interactions between *P. capensis* individuals were not always aggressive.

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6.4 DISCUSSION

My results confirmed the findings of Cooper *et al*. (1997) that *P. capensis*, together with the flat lizard, *P. broadleyi*, display the highest rates of movement (MPM and PTM) during activity of all cordylids investigated thus far (Table 1). Despite considerable variation among localities, mean PTM for *P. capensis* was consistently higher than 3% and mean MPM consistently higher than 0.7. *Pseudocordylus capensis* and *P. broadleyi*, are therefore distinct outliers in a clade that has been described as strict ambush foragers (Cooper *et al*. 1997; Mouton & Van Wyk 1997; Whiting 2007). My preliminary observations indicated that *P. nebulosus*, the sister species of *P. capensis*, probably also display high movement rates during foraging, whereas other members of the genus *Platysaurus* might also display similar high rates (Whiting 2007).

It is clear that, although falling within the PTM and MPM ranges that one would associate with ambush foraging, the Cordylidae is less homogenous a group with regard to foraging mode than what was previously thought. *Platysaurus* being basal in the family, and the shift from widely foraging to a more sedentary mode having taken place in the immediate ancestor of the Cordylidae (Cooper *et al*. 1997; Mouton & Van Wyk 1997; Whiting 2007), an intermediate condition in *Platysaurus* probably makes some evolutionary sense. The phylogenetic position of the *capensis-nebulosus* clade within the family is still uncertain and it is therefore not known at this stage whether similarities in foraging mode between this clade and *Platysaurus* are plesiomorphic or the result of convergent evolution.

Pseudocordylus capensis and *P. broadleyi* have several features in common as far as habitat, morphology, and foraging behaviour are concerned. Both species frequent extensive, barren rock surfaces, particularly, but not exclusively, at waterfalls or along water courses (Whiting 2007; Chapter 3). *Platysaurus broadleyi* is, with the exception of a

subpopulation along a tributary, restricted to the main course of the Orange River, with a large congregation at the Augrabies Falls (Branch & Whiting 1997). *Pseudocordylus capensis* is likewise a common sight at waterfalls or along rivers, particularly in the northern, arid section of its range (Chapter 3). Where it is not associated with waterfalls and rivers, it frequents large boulders and cliff faces (Chapter 3). It is expected that food (insects) will not be uniformly distributed over these large rock surfaces and that individuals will have to shuttle from their crevice shelters to areas where food availability is sufficiently high, or, on the other hand, will regularly have to change position to increase foraging efficiency. A less sedentary foraging strategy may therefore be a prerequisite for life on large, barren rock surfaces.

There are furthermore indications that fruit may be an important dietary item of *P. capensis*, similar to the situation in *P. broadleyi* where figs constitute an important dietary item (Whiting 2007). If further studies show that frugivory is well established in *P. capensis* one would probably be able to conclude that opportunistic foraging is required when living on large rock surfaces, or, on the other hand, that frugivory requires a less sedentary foraging strategy. I also noted that *P. capensis* tongue-flicks regularly during activity. In general, ambush foragers do not tongue flick and rely on visual cues for prey location (Cooper 2007). *Platysaurus broadleyi* tongue flicks extensively when foraging for figs (Whiting & Greeff 1997; Whiting 2007) and further study will tell whether *P. capensis* also makes use of tongue flicking when eating fruit.

Pseudocordylus capensis and *P. broadleyi* are also very similar in morphology. Both are built for speed, having long limbs and granular scaling, and lacking spiny armour (Losos *et al*. 2002). Losos *et al*. (2002) found that both species, when confronted, will run considerable distances before entering the safety of a crevice, in sharp contrast to more heavily armoured species of the genus *Cordylus* which will immediately take shelter.

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Being fast is clearly another prerequisite for life on large, exposed rock surfaces, and a concomitant, less sedentary foraging strategy. The morphology of these two species suggests that they are not typical ambush foragers and that they, on a regular basis, move considerable distances away from the safety of their shelters, movements which can only be related to foraging (see also Whiting 2007).

Like in the case of *P. broadleyi* (Cooper *et al*. 1997), *P. capensis* showed considerable variation in both PTM and MPM among individuals, with some individuals exhibiting values that one would associate with active foraging. The wide variation may be a reflection of the flexibility of foraging behaviour in these two species. Likewise, the considerable variation between localities indicates that *P. capensis* can adjust its foraging strategy according to local conditions. The relatively low PTM and MPM values recorded for September at Landdroskop, for example, may be the result of high food availability at the end of the rainy season.

The relatively large home ranges that I recorded for both males and females of *P. capensis* tie in with the relatively high PTM and MPM values recorded. Widely foraging lizards generally have larger home ranges than ambush foragers (Stamps 1977). No data on home ranges are available for *P. broadleyi*, but ranges are expected to be large (M.J. Whiting, pers. comm.). Limited information on home range size is available for other members of the Cordylidae. Both *Cordylus cataphractus* (Effenberger & Mouton 2007) and *C. giganteus* (Ruddock 2000) have small home ranges (smaller than 1 m^2), individuals restricting their activity to the area immediately outside the crevice (*C. cataphractus*) or burrow (*C. giganteus*). Griffith (unpubl. data) found that male *P. melanotus subviridis* have relatively large home ranges with a mean value of 189.01 ± 33.57 m^2, thus comparable to the mean values of vertical space use that we recorded for *P. capensis*. Females of *P. m. subviridis*, however, had small home ranges (13.51 ± 1.86 m^2).

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In my study, extreme variation in space use was recorded for both males and females, with values above 400 m^2 recorded for both sexes. Furthermore, vertical area of space use as recorded in my study should be a gross underestimation of actual home range. I therefore conclude that, *P. capensis* is unique among cordylids in that both males and females could potentially have large home ranges.

In both *P. m. subviridis* and *C. cataphractus* (males: 0.791 ± 0.431 m^2; females: 0.394 ± 0.249 m^2), the home ranges of males are considerably larger than those of females and also overlap with those of several females, pointing to a mating system of territorial polygyny (Effenberger & Mouton 2007; M.G. Griffith unpublished data). Both these species are sexually dimorphic in size, males being larger, with larger heads, than females (Mouton & Van Wyk 1993; Mouton *et al*. 1999). In *P. m. subviridis*, males are also brightly coloured (Mouton & Van Wyk 1993). Although areas of space use of male *P. capensis* may overlap with those of several females, there is no indication that this species has a mating system of territorial polygyny. It only displays limited sexual size dimorphism, males having slightly larger heads, but smaller body sizes than females (Van Wyk & Mouton 1998). The fact that there is only marginal overlap in the space use of males, however, does suggest that males are territorial to some degree. When little or no overlap in home ranges is found among individuals of the same sex, it is usually considered to be indirect evidence of territoriality (Stamps 1977; Rose 1982). However, highly territorial species usually display a high degree of sexual dimorphism (Stamps 1983; Shine 1989), as is also the case in *C. cataphractus* (Mouton *et al*. 1999). With the limited information available at present it is difficult to come to a firm conclusion regarding the mating system in *P. capensis*. Males are territorial and their home ranges may overlap with those of several females, but since females may also have large home

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ranges that may overlap with those of several males, there is no indication that males maintain harems in a system of territorial polygyny.

From my results it is clear that *P. capensis* is well-equipped for life on large rock formations. Large rock formations, particularly those providing an altitudinal range of microhabitats and many shady areas, may be a prerequisite for this melanistic species to survive in warm environments (Janse van Rensburg *et al*. 2009; Chapter 2). Its long limbs may be an adaptation for living on large rocks, but its less sedentary foraging strategy appears to be a preadaptation, as the same strategy is displayed by its sister species, *P. nebulosus*, which does not show any particular preference for large rock formations.

In conclusion, *P. capensis*, like *P. broadleyi*, displays a less sedentary foraging strategy in comparison to other cordylids. A less sedentary foraging strategy appears to be a prerequisite for life on large, barren rock surfaces where food availability may be low or not uniformly distributed. Both males and females of *P. capensis* may have large home ranges, in accordance with the less sedentary foraging strategy displayed by this species. Like in the case of *P. broadleyi*, fruit may be an important dietary item of *P. capensis*, but further study is needed to confirm this.

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CHAPTER 7

CONCLUDING REMARKS: MELANISM AND CONSERVATION

In accordance with the thermal melanism hypothesis, the majority of melanistic cordylid lizard species are found in cool environments in coastal or montane localities (Janse van Rensburg, Mouton & Van Niekerk 2009; Chapter 2). The small distribution ranges of these species, in cool environments may suggest that while melanism may be an advantage in cool conditions, it may be a constraint under warm conditions, thus excluding these populations from warm environments. However, in contrast to most melanistic populations, *Cordylus peersi* and the northern populations of *Pseudocordylus capensis* are found in warmer environments (Janse van Rensburg *et al*. 2009; Chapter 2), suggesting that the effects of melanism may be confounded by other factors (Clusella Trullas, Van Wyk & Spotila 2007). Although occurring in a warm environment, *C. peersi* is generally confined to cooler enclaves the warm Namaqualand region, (Janse van Rensburg *et al*. 2009; Chapter 2), and possibly not be influenced by a warmer climate to the same extent as *P. capensis*.

Data on morphology and habitat selection in melanistic cordylid species revealed that individuals of *P. capensis* and *C. peersi* differ from other melanistic cordylid species in that they have longer limbs, and that they also frequented higher rock formations (Chapter 3). *Pseudocordylus capensis* was also the least armoured of all melanistic cordylid species. In the northern part of its range, populations of *P. capensis* were exclusively associated with large boulders, cliff faces and waterfalls (Chapter 3). It was demonstrated that higher rock formations provided *P. capensis* with a thermally more suitable habitat during summer than small rock formations (Chapter 4). Some degree of shuttling was, however, required between thermally

suitable microsites (Chapter 4). Long limbs can thus be regarded as a prerequisite for life on large rocks, as short limbs would not allow for large vertical movement on high rock formations. It was concluded that a melanistic species, such as *Pseudocordylus capensis*, can survive in warm environments because its morphology enables it to utilize high rock formations that provide a range of thermal opportunities on a daily basis (Chapter 3, Chapter 4).

It is widely agreed that the Earth's climate is changing (Peters & Lovejoy 1992; Hughes 2000). Climate change is already responsible for changes in the distribution ranges of many species, and it is expected that the rate of change will exceed the ability of species to adapt to the change (Feehan, Harley & Van Minnen 2009). Small populations on islands or high on mountain tops may be particularly vulnerable to extinctions if their habitats are reduced or lost due to climate change (Allison & Leisz 2009).

The Cape Floristic Region is likely to be highly sensitive to climate change (Midgley *et al*. 2003, Hanna *et al*. 2005). Climate change models predict that the CFR will experience a 1.8°C increase in mean annual regional temperature over the next five decades (Midgley *et al*. 2003). The region is expected to become more arid and large areas of the Fynbos biome is expected to be lost along the west coast and in the Cederberg Mountains (Midgley *et al*. 2002, 2003).

Due to the constraining effect of climate on the distribution of most melanistic populations, and the increasing threat of global warming, melanistic cordylid species should be considered as priority species for conservation. In order to conserve a species it is, however, necessary to understand the dynamics of the species. Knowledge of the climatic tolerances of species can be useful in predicting potential future range changes (Hannah *et al*. 2002).

The majority of melanistic cordylid species have very small distribution ranges in cool environments, and with amelioration of climatic conditions, these ranges are likely to contract. From a climatic point of view, most melanistic cordylid species are in danger of going extinct. Populations in montane localities can be driven to higher elevations, but some populations have

no higher elevations to migrate to (*P. nebulosus*). Land area also decreases with elevation, and this can result in population declines and extinction (Allison & Leisz 2009). Coastal melanistic populations have no higher elevations they can migrate to, and they cannot migrate to the already warmer inland areas. Climate change is thus a very real threat to these species, as they require very specific climatic conditions to survive in.

Having a wide distribution and occurring successfully in warm environments (Chapter 3, Chapter 4), *Pseudocordylus capensis*, on the other hand, may be less affected by climatic changes than melanistic populations with small distribution ranges, and may be the only melanistic species that is pre-adapted for life in warm environments. While some range contraction is possible, the morphology of *P. capensis* will still enable individuals of this species to frequent rock formations that offer a range of thermally suitable microsites, thus still enabling survival in warm environments. Populations at warm lowland localities will also be able to migrate to cooler and higher elevations. Further information is, however, required on the thermal biology of *Pseudocordylus capensis*.

The Greater Cederberg Biodiversity Corridor (GCBC) (Chapter 1; www.cederbergcorridor.org.za) provides a home to at least two melanistic cordylid species, namely *Cordylus oelofseni* and *Pseudocordylus capensis*. Understanding the habitat requirements and the response to the limiting effects of climate, are central in drawing up a conservation plan for these species. This study was thus a start in obtaining the necessary information on melanistic cordylid species.

With the distinct possibility that two populations of *C. oelofseni* may be described as new species (Daniels, Mouton & Du Toit 2004), there is a high probability that there may be several more undiscovered populations belonging to this complex. Data on the climatic conditions and habitat currently associated with *C. oelofseni*, may be a useful tool in modelling distribution

range contractions and/or expansions, and also in predicting where other populations are likely to occur. This will greatly aid in the search for other isolated populations.

While *Pseudocordylus capensis* may be pre-adapted for survival in warm environments, its survival is still very much dependent on the availability of its habitat. The GCBC would thus play a vital role in the conservation of this species and its habitat as a large part of its distribution range falls within the boundaries of this conservation area. *Pseudocordylus capensis* can also play an important role in ecotourism as this is a highly visible species that is very tolerant of human presence.

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